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**SOME EARLY TERTIARY RHINOCEROSES AND
HYRACODONTS**

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ERRATA for BULLETIN 50

For *Hyrachus* read *Hyrachyus* on pages 7, 8(twice), 15, 23, 33(twice),
Table VII(three times),

For *Hyracodone* read *Hyracodon* on page 28

For LM 1 - / read LM 1 - 3 / page 104, fig. 34.

SOME EARLY TERTIARY RHINOCEROSES AND HYRACODONTS¹

By HORACE ELMER WOOD, 2ND²

Following the work of Cope, Osborn, Peterson, Troxell, and others, the time seems ripe for a revision of the Eocene hyracodonts and the earlier true rhinoceroses, from a phylogenetic standpoint. The progress of discovery since Osborn's monograph of 1898 and his paper of 1900 calls for a new survey of the lines of evolution followed; and in particular the discovery of the long-postulated Upper Eocene ancestors of the true rhinoceroses gives a new starting-point from which to consider the phylogeny of the group. The most that can be hoped for is an approach toward the formulation of the actual relationships; further discoveries will doubtless modify extensively the lines of descent drawn in this, as in all earlier attempts.

This paper includes a systematic revision, with special reference to problems of phylogeny, and the description of three new genera and seven new species. However, the extenuating plea is submitted that distinctly more names are demoted to the rank of synonyms.

It is a pleasure to acknowledge my obligations to Professor H. F. Osborn, Dr. W. D. Matthew and Mr. Walter Granger for permission to use undescribed American Museum specimens and for facilities in carrying on this study; to Prof. Osborn, Mr. Granger, Mr. H. C. Raven, Miss Jannette Lucas, Prof. J. J. Galloway, and especially to Dr. Matthew for various helpful suggestions; to Dr. J. W. Gidley for permission to use the National Museum collections and for various courtesies in connection with my visits to Washington; to Mr. O. A. Peterson for permission to use the Carnegie Museum material and for innumerable

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The drawings of the specimens in the Carnegie and the National Museums are the work of Mr. Sydney Prentice. For the other drawings I am indebted to Dr. Florence Dowden Wood. Finally, I wish to recognize most emphatically my debt to Professor William K. Gregory for first suggesting this subject and for his invaluable advice and encouragement.

In this paper I shall use the orthodox molar terminology for the molars and for the analogous (but perhaps not always homologous) elements in the premolars. It must be emphasized, however, that these terms as applied to the upper teeth are arbitrary topographic terms and do not represent the actual order of cusp development. The subject has been discussed fully by Gregory (1922).

I shall use the following classification for the rhinoceroses:

Superfamily Rhinoceroidea Gill, 1872, modified by Osborn, 1898.

Family Hyrachyidae = Hyrachyinae, Osborn and Wortman, 1892.

Family Amynodontidae, Scott and Osborn, 1883.

Family Hyracodontidae, Cope, 1879.

Family Rhinocerotidae (Rhynocerotidae Gray, 1821, corrected to Rhinocerotidae by Owen, 1845).

I agree with Scott (1913) that it would be slightly preferable to rank the rhinoceroses as a family, with the different lines as subfamilies. The other classification is firmly

imbedded in the literature, however, and has at least the convenience of giving room for still another stage in classification, above the rank of genus. It seems impossible to join the *Hyrachus* group with any one of the later lines rather than with another, nor does it seem justifiable to unite any two of the later groups more closely with each other than with the third. In the other direction, the resemblance between the Hyrachyidae and the Lophodontidae is obvious, though perhaps increased through parallelism.

Ringström (1924) once more recognizes the elasmotherees as an independent family, equivalent to the other lines, although a large part of his paper is devoted to showing that they are fairly closely related to the more typical true rhinoceroses, through the new genus *Sinotherium* Ringström (1923). If the elasmotherees constitute a family on account of their unusual bulk, the baluchitheres certainly should be considered a new order.

Superfamily Rhinoceroidea

Horns when present are epidermal structures, composed of keratinized fibers. The orbit and temporal fossa are fully confluent. There is never an antorbital depression. A diastema is present anterior to the premolars. Both upper and lower molars are lophodont. The paracone is smaller than the metacone in M 1-2/, and the ectoloph forms an acute angle with the protoloph and metaloph. M 3/ is usually triangular, due to complete or partial fusion of the ectoloph and metaloph, associated with the suppression of the posterior buttress. In the lower cheek teeth, the talonid is distinctly lower than the trigonid. The lower molars are composed of two asymmetrical crescents, the posterior limb of each being the dominant element, but the anterior limb is never completely lost. There is no posterior accessory cusp on M /3. The digital formula is IV-III to III-III.

Family Hyrachyidae

Type genus: *Hyrachus* Leidy. North American, primitive rhinocerine perissodactyls; Wind River, Bridger and Uinta; manus tetradactyl; rudimentary horns may appear; nasals not shortened, nasal incision slight; I $3/3$ C $1/1$ P $4/4$ -(3) M $3/3$; canines are tusks of moderate length; fairly long diastema; permanent premolars never molariform; ¹ upper molars with the cusps not fully fused into lophs, with the parastyles large independent cusps arising from the anterior cingulum, and usually with well-developed cristæ; posterior extension of ectoloph of M $3/$ always large; anterior limbs of lower molar crescents small.

Genera: *Hyrachus*, *Colonoceras*, *Metahyrachyus*.

Family Aymnodontidae

Type genus: *Aymnodon* Marsh. North American and Eurasian semiaquatic rhinoceroses; Uinta to Oreodon Beds; manus tetradactyl; hornless; nasals shortened; I $3-2/3-1$ C $1/1$ P $4-3/4-2$ M $3/3$; incisors originally small and progressively reduced; canines huge tusks; rather short diastema; upper premolars unprogressive and become molariform beginning posteriorly; premolars progressively overshadowed in size by the molars; upper molars have the parastyle plastered against the paracone; the posterior extension of the ectoloph of M $3/$ is always large and everted; lower molars are disproportionately long for their width.

Genera: *Aymnodon*, *Metamynodon*, *Cadurcotherium*.

Family Hyracodontidae

Type genus: *Hyracodon* Leidy. North American and probably Asiatic, cursorial rhinoceroses; Bridger to Protoceras Beds; manus tridactyl; hornless, nasals shortened. I $3/3$ C $1/1$ P $4/(4)-3$ M $3/3$; canines become incisiform and little larger than the incisors by Oligocene time; dia-

¹ The only approach being in P $/4$, where, however, the entoconid never fully fuses with the hypoconid to form a talonid crescent, except after prolonged wear.

stema rather short; P /1 reduced and lost before the Oligocene; premolars become molariform starting posteriorly; upper molars with parastyle plastered on paracone; crista usually present; M 3/ with posterior extension of ectoloph somewhat reduced but nearly always present.

Genera: *Hyracodon*, *Prothyracon*, *Triplopus*, *Ardynia* ? *Cænolophus* ?, etc.

Family Rhinocerotidae

Type genus: *Rhinoceros* Linn. North American, Eurasian and African true rhinoceroses; Bridger to Recent; manus tetradactyl to tridactyl; hornless or horned; long nasal incision; I 3-0/3-0 C 1-0/0 P 4-3/4-3 M 3/3; tusks, when present, I 1/ and I 2/; progressive mediad reduction and eventual loss of front teeth; canines always small; long diastema; premolars become progressively molariform, beginning with P /4 in the lower jaw, and with P 2/ or P 4/ in the upper jaw; upper molars with parastyle plastered on paracone and early loss of the crista; posterior extension of ectoloph of M 3/ progressively reduced in Eocene, and wanting from Oligocene on.

Genera: *Rhinoceros*, *Opsiceros*, *Elasmotherium*, *Sinotherium*, *Teleoceras*, *Baluchitherium*, *Diceratherium*, *Trigonias*, etc., etc.

No extended discussion of the European rhinoceroses has been included in this paper. Guesses as to their affinities, based on the chaotic literature, are of limited value without re-study of the specimens themselves; and, with the probable exception of that very obscure genus, *Prohyracodon*, they are too specialized in structure and too late in time to throw much light on the early Tertiary development of the North American forms. Several of the new Mongolian forms raise interesting questions, but, with the possible exception of *Ardynia*, I am, at present, inclined to regard them as side lines, which do not materially contribute to the history of the American forms.

It is desirable to re-emphasize the correction of certain mistakes in the identification of the front teeth of the true rhinoceroses. As shown by Lucas (1900), Hatcher (1901), and Peterson (1911, 1920), the following changes are necessitated:

	Corrected Nomenclature	Osborn 1898, 1923a, 1932b and others
Upper tusk is	I 1/	not I 2/
Next upper incisor is	I 2/	not I 3/
Lower tusk is	I 2 (possibly I 3)	but not C 1

In certain of his more recent papers, Osborn, by a *lapsus calami*, refers to the incisor tusks of the rhinoceroses as "the *second incisor* above and the *second incisor* below" (1923b, pp. 210, 214). A glance at *Trigonias osborni* shows that the upper tusk is the first incisor, as there are two other incisors and a canine behind it. The exact resemblance of this tooth in the genera in which it is present, from *Trigonias* to *Rhinoceros*, is convincing evidence that it is the same tooth. The lower tusk, with one tooth behind it in *Trigonias*, is most probably the second incisor, but the possibility that it is the third incisor instead must be kept in mind. The same confusion occurs in Osborn's discussion of *Baluchitherium* (1923a, p. 6), where the tusk is called the second upper incisor. Certainly in the true rhinoceroses the tusk is I 1/, in the amynodonts and hyrachyids it is C 1/ and there is no tusk in the hyracodonts. It cannot be the canine in *Baluchitherium* as there is a small alveolus immediately behind it, with the premaxillary-maxillary suture still further back. So far as these points go they tend to support Osborn's view that *Baluchitherium* belongs among the true rhinoceroses. Perhaps it descended from *Trigonias osborni*. I agree with Matthew (footnote, Osborn 1924) that "*Baluchitherium*" *mongoliense* is not a baluchithere, but more probably a coelodont rhinoceros.

Peterson (1920, pp. 453-456, pl. LXVI) has shown conclusively that in *Menoceras* (= *Diceratherium*) *cooki* dI 3 is present in the very young stage, but that the lower tusk (presumably I 2) takes over the space of both dI 2

and dI /3. The alveolus for dC /1 remains for a time shortly behind I /2 before being obliterated.

What is perhaps this same alveolus (possibly an accidental or pathological hole, however) is found on one side of a mature jaw of *Subhyracodon* (= *Aceratherium*) *tridactylum* in the American Museum, No. 543. And A. M. N. H. No. 1112, *Subhyracodon tridactylum* from the Protoceras Beds near the Cheyenne River, a young right ramus, contains the root of dI /1, the alveolus of dI /2, the root of dI /3, the alveolus of dP /1, also dP /2, dP /3, dP /4 and M /1 just cutting the gum. This is what would be expected. It emphasizes the gradual nature of the loss of teeth in the rhinoceroses.

In *Trigonias* a tooth was certainly present in the adult for a time at least, immediately behind the lower tusk. It was probably I /3 but not dI /3, if analogy with the calves described by Peterson (loc. cit.) has any bearing. It may, however, have been the canine or the deciduous canine retained.

At the suggestion of Dr. Gregory I compared the lower front teeth of *Hyrachyus* and *Hyrcodon* with the true rhinoceroses. In *Hyrachyus*, A. M. N. H. No. 12355, and *Hyrcodon*, A. M. N. H. Nos. 1491, 12460, and 14433, these teeth are sufficiently well preserved to justify comparison. In all of these I /2 accords most closely in position and character with the lower incisor tusk in the true rhinoceroses. In general this is borne out, or at least not contradicted, by all other less well preserved specimens I have seen at the American Museum and Yale Peabody Museum. In *Hyrcodon*, No. 12460 (fig. 8), this resemblance is especially striking. I /2 is set with its crown squarely across the jaw, rather than parallel or nearly parallel to it, and the crown shape has a striking resemblance to the lower tusks in *Trigonias* and *Subhyracodon*.

An additional argument is the *a priori* unlikelihood that I /3 should become the functional opponent of I 1/, the

upper tusk. All these lines of evidence taken together make it seem justifiable to regard the lower tusk as most probably the second incisor. It will be so referred to throughout the remainder of this paper.

Before describing what is regarded as a new genus of true rhinoceroses from the Eocene it is necessary to settle its relation to the Eocene hyracodonts, represented by the forms which have been referred to the genera *Triplopus* Cope and *Prothyracodon* Scott and Osborn. This necessitates a re-study of these forms.

Family Hyracodontidae Cope 1879

Subfamily Triplopodinae Osborn and Wortman 1892 =

Triplopodidae Cope 1881

Triplopus Cope 1880

Genoholotype: *Triplopus cubitalis*. Small, Eocene cursorial rhinoceroses, with a remarkably precocious cursorial adaptation, since the radius and ulna are relatively much longer compared to the other segments of the front leg than in any other rhinoceros. It differs from other rhinoceroses of the same age in the presence of an ossified auditory bulla. I ?/3 C 1/1 P 4/4 M 3/3. The canines are apparently considerably larger than the incisors. The cingulum is interrupted internally on P 3/ and P 4/. M 1-3/ have no internal cingula. M 1/ has no external cingulum. The posterior cingulum on the upper molars is never very large. The parastyles of M 1/ and M 2/ have slightly more the character of rounded, semi-independent cusps, than in the true rhinoceroses. The parastyle of M 3/ is no larger than in the Eocene true rhinoceroses, described below.

Triplopus cubitalis Cope 1880 Pl. 2, Figs. 2, 3, 4

The holotype is A. M. N. H. No. 5095, collected by Cope, in 1873, from the Lower Washakie, near South Bitter Creek, Washakie Basin, Wyoming. It was described and figured by Cope (1880a and 1885a). Further development of the specimen has brought to light a number of previously unknown characters. I $\frac{2}{3}$ C $\frac{1}{1}$ P 4 (3?)/4 M $\frac{3}{3}$. P 2-4/ are rather similar in external view. The parastyle forms a slight ridge along the anterior edge of the tooth. A depression follows, succeeded by the very prominent ridge of the paracone. The metacone forms a slight ridge which scarcely interferes with the general concave sweep of the posterior half of the ectoloph, ending with the meta-style, ridged on P 3/ and P 4/. The external aspect of M 1/ and M 2/ is similar, except that the valley between the parastyle and paracone is more pronounced. P 1/ (dP 1/ ?) is a simple blade with no internal cusps. P 2/ retains a more primitive condition than any other known member of the Rhinocerotidea, its closest resemblance being to *Eohippus* and *Homogalax* (= *Systemodon*). The external aspect resembles P 3/ and P 4/. The internal part of the tooth slopes away rapidly from the ectoloph. Besides the slope of the ectoloph, the chief internal element appears to be the basal cingulum, which rises to form two cusps, on the slopes of the paracone and metacone, respectively. The posterior is the larger of the two, and is connected with the anterior part of the metacone by a very small and insignificant "metaloph." The tooth is subtriangular. In P 3/ the protoloph and metaloph join to form a U. There are two moderately deep outlets from the median valley, of nearly the same depth, at the outer ends of the U, between the protoloph and the paracone, and between the metaloph and the metacone. The protoloph and metaloph are incipiently separated by a well-marked groove across the crest continuing down the internal face of the tooth. P 4/ has no separation whatever between the protoloph and metaloph which form an undivided U,

enclosing a deep basin. The lowest point on the ridge is between the metaloph and the metacone, at which point there is a deep outlet. There is no internal cingulum on the upper molars. M 1/ has no external cingulum. There is a crista on M 1/ but none on M 2/ or M 3/. The posterior cingulum of M 2/ is exceptionally small. M 3/ is still in the alveolus. It shows a distinct advance over the *Hyrachidæ*, but there is still a well-developed, posterior extension of the ectoloph, of somewhat the same type as in *Hyracodon*, but farther from the median line. An ossified auditory bulla is present, a structure which has not been found in other rhinoceroses of at all similar age. The manus is tridactyl. Detailed measurements are given below, as well as a more accurate and complete figure than those of Cope (1885a and 1887).

Additional development of the type brought to light a number of important new characters of the upper cheek teeth, and makes it possible to correct several mistakes in Cope's description and figures. Cope's "extra ridge" and "pot-hook" on dP 4/ and M 1/ were simply due to part of the metaloph being broken off and separated from the rest. The enormous crista-like swellings which partly blocked the valleys of M 2/ and M 3/ proved to have no certain connection with those teeth, although it is also possible that they represent a deposit of cement. If so, this is another surprisingly progressive character.

Part of a lower jaw (fig. 4), consisting of the symphysis and left ramus, accompanied by the right femur (A. M. N. H. No. 2344), from the "Middle" (probably Lower, see below) Washakie, south of Haystack Mountain, in the Washakie Basin, Wyoming, collected by Dr. Wortman in 1895, are probably referable to this species. M /1 and M /2 compare closely in character and measurements with those of the type. The dental formula for the lower teeth given above, of this genus and species, is, therefore, based on this jaw.

The jaw is long and slender, especially anteriorly. Its proportions suggest those of *Meshippus*. LC /1, RI /1, the roots of RI /2 and I /3, RC /1-P/2, RP /3 (mostly lost), and RP /4-M /3 are present. I /1 resembles I /1 of *Hyrachus* in being a broad, slightly curved, nearly transverse blade, tapering somewhat toward the root. C /1 has a rather unusual character. It is not much larger than I /1, somewhat elongated, and the antero-ventral border is recurved. The diastema is, relatively, rather long. P /1 is a simple blade with an anterior cuspule clearly defined, and a very slightly developed posterior cuspule. P /2 is functionally an antero-posterior blade, but the paraconid is slightly internal, and the protoconid and metaconid, which are almost continuous, form a blade sloping internally, at a slight angle to the paraconid. Thus the trigonid shows the faint beginning of a crescent. The talonid is a simple antero-posterior blade, lapping up on the postero-external slope of the trigonid. P /3 is broken and lost, except for the hypocone, which resembles that of P /4. P /4 is quite primitive. The trigonid crescent is well developed. The anterior cingulum surrounds the paraconid completely, starting at the metaconid, and, in an attenuated form, running completely around the anterior end of the tooth. The hypoconid is mainly a conical cusp, with an anterior extension which overlaps the trigonid. The entoconid is a small cuspule, adjoining the hypoconid, but much lower. They would not become confluent until an advanced stage of wear. The basal cingulum is very distinct, behind and internal to, the entoconid. Altogether, this tooth is very reminiscent of *Hyrachyus*. The molars are progressive. The anterior and posterior cingula are reduced. The coronoid process of the mandible is markedly recurved over the condyle.

The ventral spine of the atlas is conical, and on the central part of the ventral surface, instead of at the posterior edge, as in rhinoceroses in general. (In *Hyracodon*,

the condition is intermediate.) The odontoid process of the axis is a long peg, not confluent with the prezygapophyses. (See Cope 1885a, Pl. LVa.)

The coracoid process of the scapula is well-developed and clearly defined. There was probably a supracondyloid fenestra on the humerus. (See Cope 1885a, Pl. LVia.) If there was not an actual vacuity, the bone must have been a mere film. This condition, of course, is correlated with the straightening of the limb in a high degree of cursorial specialization, resulting in pressure of the olecranon process on the humerus and resorption of the bone. The posterior descending process of the magnum is remarkably long in proportion to the size of the animal, and the unciform has a very peculiar descending process, which is nearly as long (fig. 2).

This form is quite highly specialized, in its remarkably complete cursorial adaption for so early a time, in which it greatly exceeds *Hyracodon*, coming somewhere near the proportions of a race-horse in its front leg (see table of limb ratios below, and Gregory, 1912). It is virtually impossible for it to have been ancestral to any other known genus of rhinoceroses. However, it shows various resemblances both to *Prothyracodon*, and to the Eocene true rhinoceroses described below.

Lophialetes (Matthew and Granger, 1925c) is a remarkable form. The resemblance to *Triplopus cubitalis* in P 3/-M /3 is striking; yet P 2/ is very much more progressive, approaching P 3/ in character, and M /3 has the typical lophiodont heel. The most likely explanation is probably parallelism, on the part of a lophiodont.

Triplopus grangeri, new species Pl. 2, figs. 5, 6, 7; Pl. 4, figs. 14, 15

The holotype is A. M. N. H. No. 1972, collected near

the White River, Utah, top of Horizon B, Uinta, by Mr. Walter Granger, in 1895. I $\frac{2}{3}$ C $\frac{2}{1}$ P $\frac{2}{2}$ M $\frac{3}{3}$. The tips of the premaxillaries are appressed, but entirely separate. I $\frac{1}{1}$ is of typical hyracodont pattern, and shows no tendency toward enlargement. The cingulum is interrupted internally on P $\frac{4}{4}$ and M $\frac{1-3}{3}$. P $\frac{4}{4}$ is slightly more advanced than in *Triplopus cubitalis*, having a slight division posteriorly between the metaloph, and the proto-loph which curls around it, but none internally. The parastyles of M $\frac{1}{1}$ and M $\frac{2}{2}$ are slightly more independent than in any of the true rhinoceroses. M $\frac{2}{2}$ and M $\frac{3}{3}$ have cristæ. M $\frac{1}{1}$ is too worn to indicate whether a crista had been present or not. It has no external cingulum on the metacone. There is a very well-developed posterior extension of the ectoloph on M $\frac{3}{3}$, somewhat intermediate in character between the conditions found in *Hyrachyus* and in *Hyracodon*. The parastyle of M $\frac{3}{3}$ is like that of the new, Eocene true Rhinoceroses described below. There is an accessory ridge beside the crista of left M $\frac{3}{3}$, which is not present on right M $\frac{3}{3}$. The antero-ventral border of C $\frac{1}{1}$ is recurved, as in A. M. N. H. No. 2344, referred to *Triplopus cubitalis*. It is larger than the incisors. The lower molars are not especially distinctive.

The type consists of fragments of the upper and lower jaws, originally imbedded in a single block of sandstone. The more important fragments are: LP $\frac{4}{4}$, LM $\frac{1-3}{3}$, RM $\frac{2-3}{3}$, the back of the left ramus with M $\frac{2-3}{3}$, the corresponding part of the right ramus with M $\frac{1-3}{3}$, the badly damaged symphysis with the roots of the three left incisors, the left canine, right I $\frac{1}{1}$ (damaged), and the root of right I $\frac{2}{2}$, and the tips of both premaxillaries, with the stub of I $\frac{1}{1}$ in the left, and most of I $\frac{1}{1}$ and the stub of I $\frac{2}{2}$ in the right (figs. 5 and 6).

Carnegie Museum No. 2336 (fig. 7), from Horizon B

of the Uinta, represented by left P 3/-M 3/, should probably be referred to this species.

Carnegie Museum No. 3110 (figs. 14 and 15), from Uinta A, right P 3/-M 2' and left P /2, P /3, and M /1-3, is more doubtfully referable to this species.

These two Carnegie Museum specimens are probably referable to *Triplopus grangeri*—unless a new species be created for each—but both specimens differ somewhat from the type, and from each other.

C. M. No. 2333 retains a large root to indicate the upper canine. There were four upper premolars, the first two indicated only by their roots. P 3/ is much like the corresponding tooth of *Triplopus cubitalis*. The cingulum is interrupted internally, and the protoloph and metaloph are distinctly separated, though this separation would be obliterated after considerable wear. There is no crista. For P 4/, it is a question of definition whether the cingulum is interrupted internally or not. There is a well-developed crista. The molars have their parastyles as in the type of *T. grangeri*. The cingula are interrupted internally, as in the type, but M 2/ has a larger rudiment across the internal valley, and this is more extensively, though still very faintly, developed on M 3/. M 1/ has a large crista, M 2/ and M 3/ rudimentary ones. M 2/ is surprisingly long in proportion to its width. M 3/ is much like the type.

C. M. No. 3110 has several interesting features. The teeth are more worn than in either A. M. N. H. No. 1972, or C. M. No. 2336. The internal separation between the protoloph and metaloph of P 3/, if it ever existed, has been obliterated. Apparently, however, the protoloph coils around the metaloph, making the outlet of the valley posterior, as in most other primitive rhinoceroses. This was certainly the situation in P 4/. Neither premolar had a crista, and the cingulum was interrupted internally on each. M 1/ and M 2/ were devoid of internal cingula, except the usual rudiments at the outlet of the median valley.

Apparently M 1/ had a crista, whereas M 2/ did not. There were four lower premolars. P /2 has an antero-posterior, blade-shaped hypoconid, with a cingulum completely enclosing the talonid basin. P /3 has a similar hypoconid as the highest part of the talonid, but connecting with the entoconid, forming the ghost of a crescent. P /4 is lost, except for a small fragment, which shows the entoconid not fully joined to the hypoconid, and partly connected, by the cingulum, to the metaconid. The lower molars have no unusual features.

Epitriplopus, new genus

The genoholotype is *Prothyracodon uintense* Peterson. I ?/3, C ?/1, P 4/4-3, M 3/3. P 2/ has an ectoloph, and a single large internal cusp connected with the paracone by a cross-crest. M 2/ is very long in proportion to its width. The posterior buttress of M 3/ is lost completely, except for a trace near the base. The manus is tridactyl.

Epitriplopus uintensis (Peterson) 1919. **Prothyracodon uintense** Peterson. Peterson, 1919 Pl. 3, fig. 9

The holotype is C. M. No. 3007a. from horizon C, Uinta, Eocene, six miles east of Myton, Utah. The animal is larger than any other known Eocene hyracodont, approximating in size the new genus of Eocene true rhinoceroses described below. I ?/3, C ?/1, P 4/4-3, M 3/3. No meta-loph is present on P 2/. The cingulum is absent internally on M 1/ and M 2/, except across the median valley. M 3/ has no trace of the posterior extension of the ectoloph, except possibly at the base of the tooth, a condition otherwise unknown among the hyracodonts, except in *Ardynia*, which may be a composite form. The lower incisors and canine are much as in *Hyracodon*, except that the canine is somewhat larger proportionately. P /1 is small or missing.

As stated by Matthew and Granger (1925a), "Peterson's species can hardly be cogenetic with *P. obliquidens* (Scott and Osborn), in which M 3/ retains the free pos-

terior flange of the ectoloph, but may be comparable with *Prohyracodon* Koch of the Eocene of Hungary."

In the type skull described and figured by Peterson (1919), the deciduous premolars had not been replaced, and the crown of M 3/ would probably not have cut the gum. Cutting small windows showed that, at least, right P 2/ and left P 2/ and P 3/ were developing. At my request, Mr. Peterson very kindly had left P 2/ and P 3/ exposed. The results were disappointing, as the crowns were incompletely calcified. P 2/ shows the ectoloph, and a single internal cusp, the protocone, slightly elongated antero-posteriorly, and connected with the paracone by a cross-ridge. The protoloph is developed, therefore, but there is no trace of a metaloph. This condition is more progressive than that in *Triplopus cubitalis*; it is much less so than *Prothyracodon obliquidens*. P 3/ is an amorphous mass; its interpretation is, to say the least, problematical. DP 4/ is molariform, with both protoloph and metaloph well-developed. The internal cingulum is slightly interrupted by the protoloph, and broadly by the metaloph. In general, Peterson's figure (1919, Pl. XLV) of the type skull is excellent except that the protocone of left M 1/ has a misleading appearance, as a result of fracture, and the parastyle of M 3/ is not shown. M 1/ is a little disproportionately long for its width, and has a tendency to taper posteriorly. Both these tendencies are carried much further in M 2/, giving it a strikingly individual character, at first glance. M 1/ has a crista, M 2/ and M 3/ have not. Basal singula are present anteriorly, posteriorly and in the median valley of M 1/ and M 2/. They are absent from the rest of the internal surface, as well as from the ectoloph. M 3/ has a parastyle of moderate proportions, about as in *Triplopus cubitalis*. The top eight millimeters of the crown has no trace of the posterior buttress at all, being a perfectly smooth curve. Basally, there is an incipient ridge on which a posterior cingulum would presumably have been

deposited later. Perhaps a slight trace of the posterior buttress would also have been formed in this region. The general character of the tooth markedly suggests *Prohyracodon Koch*. M 2/, however, is entirely different in these two forms.

Peterson's figure (1919, Pl. XXXVI) is quite accurate in its representation of the type lower jaw. The second incisors are more asymmetrical than they are represented, with their median sides the longer. M /1 and M /2 have posterior cingula, which are not shown. C. M. No. 2990 is provisionally referred to this species by Peterson. The lower canines are rather large.

The following specimens have also been referred to this species by Peterson. C. M. No. 2990 includes a right radius—length 174 mm. C. M. No. 3007 (not 3097, Peterson, p. 134, line 28) includes the scapulæ and humerus. These bones are rather suggestive of *Hyrachyus*. The length of the humerus is 156.5 mm. With No. 2990, this would give the ratio $R/H = 1.11$, which is between the ratios of *Triplopus cubitalis* and *Prothyracodon obliquidens*. However, even if both specimens are correctly assigned to this species, the fact that the radius and humerus are from different individuals makes the probable error so large that the significance of this ratio is minimal. C. M. No. 3201 is doubtfully referred to this species.

The provisional reference of this form to the *Triplopodinae*, rather than to the *Hyracodontinae*, is largely based on its considerable resemblance to the Carnegie Museum specimens assigned to *Triplopus grangeri*, and on its more general resemblance to *Triplopus cubitalis*. It does not seem possible, however, to consider it cogenetic with *Triplopus cubitalis*. The character of the lower front teeth, and the reduction of P /1, appear to bar it from the *Rhinocerotidae*; and the very primitive character of P 2/ separates it distinctly from the *Hyracodontinae*.

There are some resemblances to the new Eocene forms described below. However, the small size of P 1/1 and

the character of M 3/ are quite different. And if, as is argued below, these forms are ancestral true rhinoceroses, they would, unquestionably, have had a tetradactyl manus, whereas *Epitriplopus uintensis* had a tridactyl manus.

Epitriplopus uintensis (Peterson) may have given rise to *Ardynia præcox* of Mongolia, as suggested by Matthew and Granger (1925a). In addition to the great reduction of P /2 in the Mongolian form, P 2/ in *Epitriplopus* appears to be in a much more primitive stage.

The relationships of *Ardynia* (Matthew and Granger, 1923), provided the various parts are correctly associated, are very puzzling. It does not fit definitely into any one of the families of rhinoceroses. In view of the fragmentary nature and uncertain association of the parts attributed to the type specimen, it is perhaps permissible not to consider its relationships further, at this time, than to refer its provisionally to the Hyracodontidæ.

Cænolophus (Matthew and Granger, 1925b) from the Shara Murun formation (Upper Eocene) of Mongolia, is not at all close to any American genus. The skull and feet are unknown. So far as the fragmentary dentition shows, it occupies an isolated position, not assignable definitely to either the Triplopodinæ or the Hyracodontinæ, and, possibly, not to the Hyracodontidæ. *Cænolophus obliquus* may not be cogenetic with the genotype, *C. promissus*. *Cænolophus proficiens*, Matthew and Granger (1925c), retains all four lower premolars, although P /4 is already molari-form. This combination, unique in the Hyracodontidæ, emphasizes the isolated position of this genus. Matthew and Granger refer it provisionally to the Hyracodontidæ.

Subfamily Hyracodontinae Steinman and Döderlein 1890,

correctly redefined by Osborn and Wortman 1892

***Prothyracodon* Scott and Osborn 1887**

Pl. 3, figs. 10, 11, and Scott and Osborn 1889.

The genoholotype is *Prothyracodon obliquidens* (Scott

and Osborn) 1887. Uinta hyracodonts with tridactyl manus. I 3/3, C 1/1, P 4/(4)-3, M 3/3. Canines larger proportionately than in *Hyracodon*. The basal cingulum is continuous internally around P 3/, P 4/ and the protocones of M 1-3/. There is no trace of an internal groove on the protocones of P 3/ and P 4/ (to mark an incipient separation of the hypocone from the protocone), but the protoloph hooks around the metaloph. P 2/ is subtriangular, rather than subquadrate, but much farther advanced than in *Triplopus cubitalis*. M 1/ has a distinct external cingulum on the metacone. The upper molars apparently have no cristæ. M 3/ has a distinct trace of the posterior extension of the ectoloph, of much the same character as in *Hyracodon*. P /4 and P /3 are not yet fully molariform, but suggest *Hyrachyus*, with the entoconid a separate cuspule, which does not become fully confluent with the hypoconid to form the talonid crescent, until after prolonged wear. This genus is probably ancestral to *Hyracodon*.

***Prothyracodon obliquidens* (Scott and Osborn) 1887**

Hyrachus obliquidens Scott and Osborn. Scott and Osborn, 1887, p. 259.

Prothyracodon intermedium Scott and Osborn. Scott and Osborn, 1887, p. 260.

Triplopus obliquidens (Scott and Osborn). Scott and Osborn, 1889.

Prothyracodon obliquidens (Scott and Osborn). Peterson, 1919.

The type of *Hyrachyus obliquidens* is P. U. No. 10,402, a lower jaw (for figure see Scott and Osborn, 1889, Pl. XI) with left M 3/. The type of *Prothyracodon intermedium* is P. U. No. 10,403, left upper P 3/-M 3/. M 3/ as originally present was seriously damaged and has now been sufficiently further injured so that it is impossible to check up on the published figure (loc. cit.). Fortunately, however, A. M. N. H. No. 1971 has right P 2/-M 3/, left P 4/, left M 3/, and both rami of the lower jaw, with both P /3's and P /4's and with fragments or roots of the other cheek

teeth (figs. 10 and 11). Dr. Hay left a manuscript note to the effect that this specimen represented a new species, but since it checks very closely with the lower jaw and upper M 3/ of the type of "*Hyrachyus*" *obliquidens*, and with P 3/-M 3/ of the type of *Prothyracodon intermedium*, I regard it as conspecific. I could not compare M 3/ of the latter, due to its loss, and the figure (Scott and Osborn 1889) shows some discrepancies, but I do not think they should be given serious weight. As the occlusal relations, the result of both the original structure and subsequent wear being complimentary, of the upper and lower teeth of A. M. N. H. No. 1971 are exact, there can be no reasonable question of association. For this reason I follow Scott and Osborn (1889) and Peterson (1919) in regarding *Prothyracodon intermedium* as a synonym of *Prothyracodon obliquidens*. The description will be based on all three specimens, since they supplement each other in the parts that are missing and agree closely in the parts common to any two of the specimens.

I 3/3, C 1/1, P 4/(4)-3, M 3/3. The canines are larger than the incisors. P 2/ is subtriangular, being much more primitive than in *Hyracodon* or the new true rhinoceros from the Uinta described below, but far more advanced than in *Triplopus cubitalis*. The protoloph runs postero-internally and joins the metaloph. There is a small internal cingulum on the protoloph which is not fully continuous with the anterior cingulum and does not surround the postero-internal part of the tooth at all. P 3/ and P 4/ are similar to each other, with the protoloph hooking around the metaloph, leaving a posterior outlet for the median valley in the unworn tooth, and with a continuous cingulum around the anterior, internal and posterior sides. There is no crista on any of the upper molars. M 1/ and

M 2/ are rhinocerotid. The basal cingula surround their protocones anteriorly and internally. M 1/ has a distinct external cingulum on the metacone. M 3/ has a complete cingulum anteriorly, internally and posteriorly, but it is rather faint internally. The parastyle is slightly more prominent than in *Hyracodon* and much more than in *Triplopus* or the true rhinoceroses. The posterior extension of the ectoloph is present, slightly less prominent than in *Triplopus cubitalis* or the type of *Triplopus grangeri*. P /1, when present, is very small. P /2 is known only from the roots. It was of normal size. P /3 is not yet molariform, since the entoconid is a separate cuspule, not connecting with the hypoconid to form the talonid crescent until an advanced stage in wear. The anterior cingulum is weak but complete. P /4 is similar in structure but its proportions are more molariform and the anterior cingulum is both complete and distinct. Both these teeth are more advanced than in *Hyrachyus*. There is nothing diagnostic about the lower molars.

The manus is known to be tridactyl, from the manus associated with the type (Scott and Osborn 1889). Peterson (1919) described two fore legs, with similar wrist bones, which he refers to *Prothyracodon obliquidens*. The limb ratios differ so markedly from *Triplopus cubitalis* that it is improbable that they could belong to *Triplopus grangeri*, the only other known Uinta tridactyl rhinoceros of about the right size. In the table of limb ratios therefore, this specimen is indicated as *Prothyracodon ? obliquidens ?*. The ratios are rather similar to *Hyracodon apertus*, as would be expected.

The important differences from *Triplopus* in *Prothyracodon* are: the ratios in the front leg, the presence of internal cingula on the molar protocones, the absence of an ossified auditory bulla, the absence of cristæ, the much greater progressiveness of P 2/, the greater progressiveness of P 4/, the greater reduction of the posterior buttress of M 3/.

C. M. No. 3201, the skull figured by Peterson (1919) and provisionally referred to this species, is probably correctly assigned. I 3/?, C 1/1, P 4/3, M 3/3. It has a striking resemblance in general character to *Hyracodon*. As its condition is such that it is unsafe to separate the upper and lower jaws, it is not possible to state definitely that it is not *Triplopus grangeri*.

Prothyracodon obliquidens would seem to have the characters to be expected in the ancestor of *Hyracodon*. The internal cingulum is better developed on M 1-3/ than in *Hyracodon*, though there appears to be a very large range of individual variation in this respect in *Hyracodon*.

Hyracodon Leidy 1856

The type of the genus is *Rhinoceros nebraskensis* (Leidy). American, Oligocene, cursorial rhinoceroses; I 3/3, C 1/1, P 4/3, M 3/3; P 2/ is rectangular, with protoloph and metaloph parallel but not fully separate; M 3/ retains a small posterior buttress near the postero-lingual corner of the tooth; the three lower premolars are molariform; medium size; manus tridactyl. The most recent papers on the genus by Troxell (1921), Sinclair (1922) and Wood (1926) indicate that the following species are well established.

Hyracodon petersoni Wood, Titanotherium Beds, has no molariform upper premolars. The median valleys of P 3/ and P 4/ open widely to the rear, the hypocone being firmly attached to the protocone.

Hyracodon arcidens Cope, Titanotherium and Oreodon Beds, has no molariform upper premolars. The protoloph curves around the metaloph in P 2/—P 4/, coalescing, after slight wear, into a continuous crescent. *H. priscidens* Lambe, *H. arcidens mimus* Troxell, and *H. selenidens* Troxell, are probably inseparable from this species. Morphologically, the types of *H. petersoni*, *H. priscidens*, *H. selenidens*, and *H. arcidens*, form an excellent series, with the only marked break between *H. petersoni* and *H. priscidens*.

Hyracodon nebraskensis (Leidy), Oreodon and Protoceras Beds, has the protoloph and metaloph of P 4/ parallel, but intimately joined by a "mure." The hypocone is now more closely attached to the metaconule than to the protocone.

Hyracodon apertus Sinclair, Oreodon and Protoceras Beds, has the protoloph and metaloph of P 4/ only, separate and parallel.

Hyracodon leidyanus Troxell, Protoceras Beds, (earlier range doubtful) has the protoloph and metaloph of both P 3/ and P 4/ separate and parallel.

The method of metamorphosis of the upper premolars in this subfamily, presents some interesting features. In P 2/-P 4/ of *Prothyracodon*, the protoloph, consisting of the protocone and protoconule, is the main transverse crest, the metaconule forming a lower, minor crest abutting against the protocone. Then the protocone elongates antero-posteriorly, looping around the internal edge of the metaconule, and an incipient split appears to delimit the hypocone from the protocone, the median valléy opening posteriorly. This condition is found in *Hyracodon petersoni*. Here P 2/ is the most progressive, with P 3/ and P 4/ about equally advanced. Then the hypocone unites with the metaconule, while still attached to the protocone, forming an enclosed basin in *Hyracodon arcidens*. The metaconule attaches itself to the rear or middle of the hypocone loop. Thereafter, first P 4/ and then P 3/ catch up with, and pass, P 2/, which remains virtually unchanged. In *Hyracodon nebraskensis* the protoloph and metaloph of P 4/ are parallel and separate, except that they are intimately joined by a "mure"; which, in this case, is simply the remains of the protocone-hypocone connection; in *Hyracodon apertus*, the metamorphosis of P 4/ is complete; and in *Hyracodon leidyanus*, P 3/ also has become molariform. In this stage the hypocone is attached to the metaconule alone. Sinclair (1922) has shown that the gen-

eral stratigraphic succession of these forms accords closely with their apparent phylogenetic relationships; and Troxell's reference of the type of *Hyracodone leidymanus*, which was collected in the "old days," to "Middle or Lower Oligocene" is insufficient evidence to extend the known range of this species much below the Protoceras Beds, to which Sinclair (1922) refers a specimen to this species.¹

The anterior part of the trigonid sometimes forms a supplementary loph in itself in dP /2 and more especially in dP /3, in many of the early rhinoceroses. In two specimens of hyracodonts (a young hyracodont, C. M. No. 318, collected by Mr. O. A. Peterson from the Titanotherium Beds, Sand Creek, Sioux County, Nebraska, and a young *Hyracodon* sp., C. M. No. 3581, collected by Mr. O. A. Peterson from the Oreodon Beds, Bad Land Creek, Sioux County, Nebraska), this "paralophid" approaches, in size and distinctness, the metalophid and hypolophid (figs. 12 and 13).

Family Rhinocerotidae Gray, 1821

Eotrionias, new genus

The genoholotype is *Eotrionias rhinocerinus*, new genus, new species. *Eotrionias petersoni*, new species, is referred to this genus. The generic name from *ἠώς*, dawn, + *Trionias*, refers to its geological horizon and to its apparent possession of all the characters needed for an ancestor of *Trionias*.

¹ Since sending this paper to the editor, I came across an article by Prof. Othenio Abel, "Die Molarisierung der oberen Prämolaren von *Hyracodon nebrascensis* Leidy," *Paleont. Zeit.*, VIII, 3, p. 224-245, Oct. 9, 1926. We agree as to the course of premolar metamorphosis in *Hyracodon*. P 2/ of *Hyracodon leidymanus* is not yet fully metamorphosed, Troxell's figure to the contrary; his type specimen, and Sinclair's and Abel's referred specimens, all have a mure crossing the valley between the protoloph and metaloph. The Vienna specimen is from Sheep Mountain, and, therefore, probably from the Oreodon or Protoceras Beds. I do not regard Prof. Abel's revised nomenclature of the species of *Hyracodon* as an improvement, and much of it is definitely untenable from the point of view of priority.

I ?/?, C ?/?, P 4/?, M 3/3. These are Upper Bridger and Uinta true rhinoceroses, with the parastyles of the upper molars reduced to ribs on the paracones as in later true rhinoceroses.

P 4/ resembles *Trigonias osborni* in general character. The protoloph curves around behind the metaloph, so that the median valley escapes posteriorly. There is a small internal groove on the protocone, indicating an incipient separation of the hypocone from the protocone, and the cingulum is interrupted internally. M 1/ and M 2/ are typically rhinocerotid. They have no trace of an internal cingulum except at the outlet of the median valley. M 1/ has a marked external cingulum on the metacone. M 3/ shows a progressive reduction of the posterior extension of the ectoloph from a condition more primitive than *Triplopus grangeri*, in the Bridger species, to a condition scarcely more primitive than that seen in some specimens of *Trigonias osborni*. It has no crista.

If the relationships of this genus are correctly inferred, it presumably had a tetradactyl manus and a dental formula of I 3/3, C 1/?, P 4/4, M 3/3. It is very unfortunate that the structure of the manus and front teeth of the members of this genus is unknown. When they are discovered, they will furnish a valuable check as to the phylogenetic bearings of this form.

***Eotrigonias petersoni*, new species**

Pl. 4, fig. 16

This species is based on A. M. N. H. No. 2341, consisting of left P 4/-M 3/, from the "Middle" Washakie, south of Haystack Mountain, Washakie Basin, Wyoming, collected by Mr. O. A. Peterson in 1895 and previously identified as "*Hyrachyus*." The specific name is given in recognition of the many services of the collector to vertebrate paleontology.

This is an Upper Bridger ? primitive rhinoceros, with the parastyles reduced to ribs on the paracones. In P 4/ the protoloph overlaps the metaloph, allowing the median

valley to escape posteriorly. There is an incipient internal division on the protocone, hinting at the future separation of the hypocone from the protocone. The cingulum is widely interrupted internally. M 1/ is typically rhinocerototic. There is no trace of an internal cingulum, except a small cusplule on the flank of the hypocone near the outlet of the median valley. There is no definite evidence of a crista but the tooth is well worn and a slight swelling may indicate that one was present in the unworn tooth. There is a well defined external cingulum on the metacone. M 2/ is also rhinocerototic. It has a small crista. The only trace of an internal cingulum is that partly blocking the median valley. M 3/ shows a marked advance over any known member of the Hyrachyidæ in reduction of the parastyle and in the tendency to flatten out the posterior extension of the ectoloph, which, however, is still large. It is more advanced than *Prothyracodon* in the former character. It resembles *Triplopus* in the shape of the posterior buttress and post-fossette, and in the complete absence of an internal cingulum, differing from *Prothyracodon obliquidens* in both these characters.

This form might be mistaken at first glance for *Hyrachyus*, to which genus it was previously referred. It is more like *Prothyracodon obliquidens*, and still more like *Triplopus grangeri*. It shows little real resemblance to *Metahyrachyus bicornutus* Troxell, from which it differs in the less precocious P 4/, the greater reduction of the parastyles, and the ridge-shaped posterior extension of the ectoloph, instead of the more cuspidate type found in the Hyrachyidæ. It is not placed in the genus *Triplopus*, on account of its still closer resemblance to *Eotrigonias rhinocerinus* (fig. 17) in the shape of P 4/, the reduction of the parastyles of M 1/ and M 2/, and the almost exact identity in size. It fulfills all the requirements, so far as its fragmentary condition shows, for ancestry to *Eotrigonias rhinocerinus* and all later true rhinoceroses.

The level of this specimen was recorded as "Middle Washakie," before the stratigraphy of that formation had been cleared up by Granger (1909). Dr. W. D. Matthew states (verbal communication) that considering the matrix and the ideas on stratigraphy current at the time the specimen was collected, it is probably from the Lower Washakie of Granger, equivalent to the Upper Bridger of the standard continental section.

Eotrigonias petersoni differs from *Triplopus* in its larger size, the incipient internal division of the protocone and the character of the metaloph of P 4/, and in having less reduction of the crista in the molars. If it is correctly assigned to *Eotrigonias*, it also differed in other special characters of that genus, besides those visible on P 4/-M 3/. The absence of an internal cingulum and the general shape of the posterior buttress of M 3/ are approximated in *Triplopus grangeri*. The internal cingulum, however, shows a still closer resemblance to *Eotrigonias rhinocerinus*; and the difference in the specialization of M 3/ is not more than could reasonably be expected in an Upper Bridger ancestor of the Uinta species. The general morphological resemblance to *Triplopus* may well be, in part at least, due to parallelism. It differs from *Eptriplopus wintensis* in the proportions of M 1/ and M 2/, its more primitive M 3/ and its earlier geological level.

Eotrigonias petersoni differs from *Prothyracodon obliquidens* in its earlier geological level, its larger size, in the incipient internal division of the protocone of P 4/, in the almost entire absence of an internal cingulum on P 4/-M 3/, in the greater reduction of the parastyle of M 3/, and in the greater primitiveness of the posterior buttress of M 3/.

The assumption here made of a tetradactyl manus is utterly without direct proof, but the extraordinary resemblance of this species to *Eotrigonias rhinocerinus* is so striking, except in the character of M 3/, that it seems out of the question to refer it to either *Triplopus* or *Prothy-*

racodon. It certainly does not belong to *Hyrachyus*, nor to the Hyrachyidae. It might be difficult to separate it generically from *Triplopus*, except for the strong probability that it is definitely on the true rhinoceros side of the fence, that P 2/ was very different, and that the manus was tetradactyl. Whether the front teeth already show rhinocerine affinities is much more doubtful, but it seems likely that already I 1/ and I 2/ were specialized in the direction of their future lines of progress, and that the canines were no larger than the third incisors.

A. M. N. H. No. 19231, consisting of left P 3/—M 3/ and the right femur, collected by Mr. Miller of the Expedition of 1922 from horizon B3, Bridger, Cottonwood Creek, Bridger Basin, Wyoming, may belong to this species. Its general appearance would warrant this reference. Unfortunately, every diagnostic character that would definitely settle its affinities as between *Eotrionias* and *Hyrachyus* was destroyed, apparently in shipment. There are internal cingula on P 3/—M 2/. There is a collector's note that the specimen had a peculiar M 3/, which is suggestive of *Eotrionias petersoni*, rather than of any hyrachyid. This is of importance only as a plausible suggestion of a possible downward extension of the range of *Eotrionias*.

Eotrionias rhinocerinus, new species Pl. 4, figs. 17, 18, 19

The holotype, Y. P. M. No. 13331, was collected by Messrs. Smith and Heisey, August 8 or 9, 1874, near the mouth of Lake Fork, in the Uinta Basin. It was mixed, perhaps in unpacking, with fragments of *Hyrachyus* sp., including right M 2/—M 3/, and with left P 3/—M 2/ of *Homogalax uintensis* Troxell.¹

¹ With the specimen are two separate field labels: "Rare Lake Fork Aug 8th / 74 J Heisy" and "Very Rare Lake Fork Aug 9th / 74 Sam Smith." The corresponding part of Smith's report to Marsh is as follows:

"Sept. 1874.

Catalogue of Fossils from Lake Fork Uinta valley									
Aug. 1st	Very Rare	Du Shien	near the mouth	[= Du Chesne]					
" 8th	gar Pike	near the mouth	Lake Fork	15 miles south of					
		[south-west]	agency	[= Uinta Indian Agency]					
" "	Rare	"	"	"	"	"	"	"	"
" 9th	Very Rare	"	"	"	"	"	"	"	"
" "	" "	"	"	"	"	"	"	"	"
" "	Crocodile	"	"	"	"	"	"	"	"

I ?/?, C ?/?, P 4/?, M 3/3. The paracone and metacone appear as well-defined ribs on the lateral aspect of P 2/-M 3/. The internal cingulum is complete on P 2/ and P 3/, interrupted on P 4/, and absent on M 1-3/. P 1/ is represented by part of the alveolus. It was probably of fair size. P 2/ is the most advanced premolar, with the protoloph and metaloph pretty well separated from each other. The protoloph is not yet firmly attached to the paracone and slants slightly more to the rear than in the Oligocene forms. The hypocone was a conical cusp, with the metaloph attached to the anterior end. The tooth is subquadrate, as in the true rhinoceroses, not subtriangular, as in *Prothyrocodon* and *Triplopus*. In general this tooth shows a close approach to the more primitive Oligocene rhinoceroses. In P 3/ the protoloph and metaloph are confluent, with an internal groove incipiently separating the hypocone from the protocone, much as in *Trigonias osborni* (fig. 24). The tooth is sufficiently worn so that it is impossible to state definitely whether the outlet of the median was posterior or internal. On right P 3/ the cingulum is very briefly interrupted internally; it is uninterrupted on left P 3/. In P 4/ the protoloph swings around posterior to the metaloph, which is in contact with it. There is a posterior outlet for the median valley, as in

Fossils are very Scarce in this Country and very Rotten.

Sept. 20th

Yours Very Respect
Sam'l Smith"

From August 19-23 they collected from the White River near the mouth, and from September 1-17, from "Loan" Tree, Henry's Fork, Bridger Basin, Wyoming. There seems, therefore, absolutely no reason to doubt either the Uinta age or the geographic locality of the fossils. Two subsequent rough labels state "Wyoming," but these can be disregarded.

This would seem to be one of the few cases when the rather frequent diagnosis of one of the early collectors, that the fossil was very rare, had eventually turned out to be correct.

This specimen had been tentatively identified as *Hyrachus bairdianus* and later as *Hyrachus affinis*.

many of the Oligocene rhinoceroses. Its protocone is notched internally also, much as in *Trigonias osborni*. On M 1/–M 3/ the only trace of the internal cingulum is the small shelf at the outlet of the median valley. There is no trace of a crista, but M 1/ and M 2/ are sufficiently worn so that this is no proof of its absence, especially as regards M 1/. The parastyles are reduced to their proportions in Oligocene true rhinoceroses. M 1/ and M 2/ are typical primitive rhinoceros molars. M 1/ has a well-defined external cingulum on the metacone. M 3/ is scarcely more primitive than some specimens of *Trigonias osborni* (fig. 23), the posterior extension of the ectoloph being a swelling rather than a ridge. Rudiments nearly as well defined occur in various American Oligocene rhinoceroses, and in the third left upper molar of *Baluchitherium grangeri*. In *Eotrigonias rhinocerinus* this structure is present on both sides, about equally well defined. The post-fossette is prominent, due to the enlarged base of the posterior buttress, together with a well-developed posterior cingulum. The lower molars are similar to those of Oligocene true rhinoceroses. The posterior cingulum of M /3 is reduced to very small proportions.

The specimen consists of left P 2/–M 3/, right P 3/–M 3/ (all damaged except M 3/), and part of each ramus of the lower jaw, containing M /1–3. There are also a few *Hyrachyus* lower cheek teeth, a few doubtful fragments, and P /3–M /2 of *Homogalax uintensis*. Fortunately, there is no question of the association of the teeth of the type. The upper teeth are identical on both sides, and the occlusal relations, the algebraic sum of the original size and pattern, and the subsequent wear, are exact.

There is some resemblance to the *Hyrachidæ* in the external ribbing of the upper cheek teeth. On the other hand, slight changes—obliteration of the trace of the posterior buttress, and increase in size, would give *Trigonias*.

Although this form is still near the parting of the ways, it is definitely on the true rhinoceros side of the line. This is emphasized by both its resemblances to, and its advances on, *Eotrionias petersoni*.

On the basis of Koch's inadequate figures of a badly damaged specimen, it is difficult to separate this form, generically, from *Prohyracodon orientale* Koch. The measurements are very similar. On the other hand, it seems very unsafe to refer an American form to a Transylvanian genus on such tenuous grounds. It differs from *Prohyracodon orientale* in the presence of a probably rather more pronounced rudiment of the posterior extension of the ectoloph of M 3/. Both species have a posterior cingulum on M 3/. Other characters are difficult to detect, owing to the damaged character of the type of *Prohyracodon orientale*, but the following are apparent differences: the much shorter length of P 3/ and P 4/ in the American form, and the much greater length of M 2/ in the European form, which, in this character, approaches *Epitriplopus uintensis*. If I have interpreted Koch's figures correctly, both P 3/ and P 4/ of *Prohyracodon orientale* are more advanced than P 4/ of *Prothyracodon obliquidens* or even P 3/ and P 4/, respectively, of *Eotrionias rhinocerinus*, in a greater tendency toward separation of the protoloph and metaloph.

Eotrionias rhinocerinus differs from the type of *Prothyracodon intermedium* (P. U. No. 10,403), in the greater size, absence of an internal cingulum around the protocones of the upper molars and its interruption, internally, on P 4/, and in the presence of an incipient internal groove on the protocone of P 4/.

Eotrionias rhinocerinus differs from the type of *Prothyracodon obliquidens* (P. U. No. 10,402) in having a much longer tooth series.

It differs from *Epitriplopus uintensis* in having a metaloph less recurved posteriorly on M 2/, and in having M 1/

and M 2/ of normal proportions.

The two new forms, *Eotrigonias petersoni*, and *Eotrigonias rhinocerinus* compare so exactly, not only in the characters mentioned, but in the impression due to the sum total of their characters, with *Trigonias* and the true rhinoceroses, rather than with the Eocene hyracodonts, that I feel no hesitation in assigning them to the Rhinocerotidæ, even in advance of any knowledge of their front teeth or fore-feet. *Eotrigonias rhinocerinus* will probably be found to have four digits in the manus, and the full placental complement of teeth, with the canines no larger than the third incisors and 1 1/ and 1 /2 enlarged to form the tusks. *Eotrigonias petersoni* should also prove to be tetradactyl, and its front teeth should prove to be less specialized.

Eotrigonias rhinocerinus is perhaps already a shade too far advanced to have given rise to the *Trigonias* line. The general resemblance, however, is so great, that it seems rather probable that they are more closely related than by common descent from *Eotrigonias petersoni*, and that the split had occurred not long before.

Eotrigonias rhinocerinus shows a striking morphological resemblance to *Hyracodon petersoni*. The chief differences that can be stated definitely in words are the absence of a cingulum, internally, on P 4/, and the greater reduction of the posterior buttress of M 3/, in the former. However, in many minutiae, *Eotrigonias* suggests *Trigonias*, whereas the hyracodont affinities of *Hyracodon petersoni* are unquestionable.

Prohyracodon Koch 1897

A small true rhinoceros, from the "Middle Eocene" of Transylvania. None of the premolars are molariform. In M 3/ the ectoloph and metaloph are almost completely confluent, with little trace of the posterior extension of the ectoloph.

This genus is based on *Prohyracodon orientale* (Koch) 1897.

The generic name is based on what is almost certainly a misconception of its relationships. The name is unfortunate, especially as it is easily confused with *Prothyracodon* Scott and Osborn 1887, which really is a member of the Hyracodontidæ.

Prohyracodon orientale (Koch) 1897.

Prohyracodon orientalis Koch. Koch, 1897.

Prohyracodon orientale (Koch). Abel, 1910.

A small rhinoceros from the "Middle Eocene" of Transylvania. [The Eocene age of this form has been questioned by Stehlin, and Abel (1910). A recent letter from the Hungarian Geological Survey states that, so far as they know, Koch's determinations are still valid. Prof. J. J. Galloway of Columbia University has interpreted the lists of fossil invertebrates that overly and underly the level from which *Prohyracodon* comes as being Lutetian and Ypresian, respectively. This would indicate, for *Prohyracodon*, an age about equivalent to lower middle Eocene.]. The animal is slightly smaller than *Hyracodon*. Length of M 1-3/ is 50 mm. (fide Koch). In P 3/ and P 4/, the protoloph and metaloph form a single v-shaped ridge, incipiently separated by a small notch at the apex. The internal cingulum is complete on P 3/, obscure in the figure of P 4/, absent on M 1-3/. The internal cingulum on M 2/ in Abel's reproduction of Koch's figure is apparently due to misinterpretation. The posterior buttress of M 3/ seems to be nearly lost.

Further comparison of Koch's type with *Epitriplopus* and *Eotrigonias* would be desirable. A new drawing of his type is essential.

In the table of measurements that follows, as well as in the other tables throughout this paper, I am responsible for all measurements unless the contrary is explicitly stated. Even where measurements had been published previously, it seemed desirable to obtain strictly comparable

measurements. Wherever possible, measurements from both sides of the animal are given, to serve as a check on each other, and to indicate the very large amount of variation possible in the individual, thereby giving the minimum range of variation for the species. All measurements are in millimeters.

The genus *Trigonias* is in need of revision. Lucas' original description of the genus (1900), based on rather scanty material, lacks figures or description of the cheek teeth; and valuable new material, collected since Lucas (1900) and Hatcher (1901) discussed this genus, is still undescribed. This very primitive true rhinoceros furnishes an excellent starting place for an attempt to reconstruct the phylogeny of the later forms. It is, therefore, possible to give, with more certainty than previously, the generic characters of *Trigonias* as well as the specific characters of *Trigonias osborni*. The definitions of Lucas, Hatcher and Troxell for this genus and of the various authors for the other genera and species discussed have been so much modified that it seems best to present them without quotation marks or asterisks.

Trigonias Lucas 1900

Genoholotype: *Trigonias osborni* Lucas, U. S. Nat. Mus. No. 3294. Locality: South Dakota. Age: Titanotherium Beds (Chadron Formation).

The skull is elongated, chiefly anterior to the orbit. The premaxillæ are very closely appressed and may be more or less suturally connected. The nasals and premaxillæ are very long. Hornless. I 3/3, C 1-0/0, P 4/4, M 3/3. The front teeth, except I 1/ and I 1/2, are nearly functionless. P 1/ is large for a first premolar and P 3/ and P 4/ are never fully molariform, their hypocones being principally attached to the protocones. The frequent presence in *T. osborni* of a posterior buttress (the remains of the posterior extension of the ectoloph) on M 3/ tends to unite this genus, through *Eotrigonias*, with the other lines, breaking down one of the chief family distinctions. In *Trigo-*

Table I a

[illegible]

	R	L	P. obliquidens ? of L. K'w'giri ? C.M. 3201	Prothyrocodon intermedius Holotype P.U. 10403	Prothyrocodon chiluidens Holotype P.U. 10402	Prothyrocodon oblivius A.M.N.H. 1971	Hyracodon zetterae? Holotype C.P. 5872
(d = deciduous)							
(e = estimated)							
Across zygoma							
Fax to condyle			20.0				
Nasals to occipital crest							
Height occiput above condyle							
Width between P2's							
Width between M2's							
P1 - M2							
P2 - M2							
P1 - d			72.0				
P2 - d							
M1 - d			29.4				
Heartens			47.6				
Length P1			13.8				
Width P1							
Length P2							
Width P2							
Length P3							
Width P3							
Length P4							
Width P4							
Length M1							
Width M1							
Length M2							
Width M2							
Length M3							
Width M3							

Table II

[illegible]

nias, as in all other rhinoceroses except the hyrachyids, the paracone and metacone are completely fused to form the ectoloph, and the parastyle is plastered on the paracone, in wide contrast to the well-marked separate cusps in *Hyrachyus*. The manus is tetradactyl, digit V being rather smaller, proportionately, than in the tapir.

I follow Lucas and Hatcher in identifying the only constantly missing tooth in *Trigonias* as C /1 rather than I /3. This may be erroneous (see above) but is probably correct.

Hatcher's idea of the excessive elongation of the skull in *Trigonias* was somewhat exaggerated. It was founded on the crushing and distortion of Carnegie Museum No. 95 (No. 96).

Trigonias osborni Lucas 1900

Pl. 5, figs. 20-28

Trigonias osborni Lucas. Lucas, 1900.

Trigonias osborni Lucas. Hatcher, 1901.

Cænopus platycephalus nanolophus Troxell ? Troxell, 1921a.

Trigonias tetradactylum Osborn. Osborn, 1923b.

I 3/3, C 1/0, P 4/4, M 3/3. The incisive foramen is large. The premaxillaries are closely appressed but not really suturally connected in the type specimen. None of the upper premolars are yet submolariform. The hypocone of P 2/ is well developed but still widely confluent with the protocone. There is no hypostyle on the upper premolars. On P 3/ and P 4/ the protocone and hypocone are absolutely confluent well above the cingulum, and the median valley escapes posteriorly, until, after prolonged wear, it becomes an enclosed basin, due to the confluence of the hypocone and the metaconule. There is little or no trace of an internal groove on P 3/ and P 4/ to separate the protocone and hypocone. There is little or no trace of an internal cingulum on M 1-3/. The ectoloph and metaloph of M 3/ form a very wide obtuse angle. There is a well developed posterior cingulum on M 3/ and usually a small posterior buttress, the remains of the posterior extension of the ectoloph, which recalls the condition in *Eotrigonias*,

the hyracodonts and even *Hyrachyus*. The lower premolars are increasingly molariform posteriorly. P /4 is virtually molariform except that an extension of the entoconid as a low cingulum usually blocks the inner end of the talonid valley. P /3 is well advanced. P /1 and P /2 function mainly as antero-posterior blades. P /2 resembles P/1 in character more than it does P /3. I /2 has a sharp ridge on the median side but is usually smooth or nearly so on the outside. The posterior margin of the nasal incision is vertically above the posterior border of P 2/.

This species, the genotype, was described by Lucas in 1900, being founded on U. S. National Museum No. 3924 (figs. 20 and 21), with U. S. National Museum No. 4815 as paratype (fig. 25). The type is the snout of an old individual with the three incisors, canine, and first three premolars on the right side, the third incisor, the alveoli for the other front teeth, and the first three premolars on the left side. Its only ascription is to the "Miocene" of Washington County, South Dakota. It was presumably collected by Hatcher. Lucas undoubtedly mistook a break for the upper part of the premaxillary-maxillary suture, figured in his original description (1900) and reproduced by Scott (1913).

Lucas' paratype, U. S. National Museum No. 4815, collected by Mr. J. B. Hatcher, 1886, in Washington County, South Dakota, consists of the complete left ramus with all the cheek teeth, and the symphysis, with both incisor tusks, the first incisors being represented by their roots and the third incisors by their alveoli. It is a mature individual, with the teeth well worn. The stage of advancement of the premolars agrees exactly with the other lower jaws ascribed to *Trigonias osborni*. The ridge on the outside of I /2, distinctly less developed than in the other specimens, gives this tooth a character somewhat intermediate between other representatives of *Trigonias osborni* and the lower jaw, A. M. N. H. No. 13226 b, belonging to one of the larger species of *Trigonias* described below; most of the

measurements accord closely with the other specimens of *Trigonias osborni*, but the size of the jaw and a few tooth measurements accord more closely with the larger lower jaw mentioned above. The entoconids of P /3 and P /4 are not yet fused with the rest of their posterior crescents but are separate, distinct cusps. It seems best on the whole to refer it tentatively to *Trigonias osborni*.

Hatcher correctly assigned to this species Carnegie Museum Nos. 95 (96), 97, and 98, from the Lower Titano-therium Beds, three miles north of Warbonnet Ranch, Sioux County, Nebraska, collected in 1900 by Messrs. Hatcher and Utterback. He described and figured all these specimens (1901). Carnegie Museum No. 98 may be regarded as the plesiotype. There is a conflict between Hatcher's description and the actual numbering and cataloguing of the specimens. Carnegie Museum No. 97 is, as stated, the lower jaw of a young individual and No. 98 is also correctly referred to. But Hatcher's "No. 96" is the skull actually labeled No. 95 and mounted with the composite skeleton but recorded separately as No. 96 in the catalogue.

Skull No. 95 (96) is nearly complete but much distorted and elongated by crushing. The teeth are greatly worn and several are lost. The following teeth are represented: Right: I 1/, P 2/-M 3/, alveoli of I 2/, I 3/, C 1/, roots of P 1/; Left: I 1/, P 2/, P 4/-M 3/, alveoli of I 2/, I 3/, C 1/, P 3/, roots of P 1/.

Skull No. 98 has more parts actually missing but it is not greatly distorted. P 2/-M 3/ of both sides are present in good condition. The top and front of the skull are restored in plaster (fig. 24, and Hatcher 1901).

The premaxillaries in No. 95 were apparently united in life by a tongue and groove suture, the tongue and groove running obliquely forward and upward along their appressed median surfaces. There was doubtless also a ligamentous connection but the two bones were not coossified.

As restored they are not in contact but this is quite certainly the result of distortion. There is a strongly marked sagittal crest. The individual was old and the teeth are greatly worn. On the right M 3/ of this specimen there is a well marked posterior extension of the ectoloph (fig. 22), somewhat exaggerated in distinctness by a coincident break, and a distinct trace of it on the left side (fig. 23). There is also a very slight trace of it on No. 98 (fig. 24 and Hatcher, 1901). All this suggests the condition in *Eotrigonias*, the hyracodonts and even, less markedly, in *Hyrachyus*. (See Hatcher, 1901, p. 138. He is in error in saying that the metacone is not present in M 3/.) This is a very important character phylogenetically and helps to connect the true rhinoceroses with the other rhinocerine lines. The remnant of this posterior extension of the ectoloph is often found in "*Cænopus*" *platycephalus*. A specimen of *Subhyracodon tridactylum*, A. M. N. H. No. 8088, collected from the White River Oligocene of White Buttes, N. D., by Cope in 1883, has this same type of buttress, very well developed, on both M 3/'s, but closer to the mid-line than in the ancestral forms. A possible reversion in this direction (although the buttress is much closer to the mid-line), appears on the left of M 3/ of a *Menoceras* (*Diceratherium*) in a corner of the Agate Springs Quarry block in the Carnegie Museum, in Carnegie Museum No. 1555 (figured by Peterson, 1920, pl. LVIII), and on the right M 3/ of *Menoceras*, A. M. N. H. No. 14229.

To *Trigonias osborni* must also be referred Carnegie Museum No. 3914a, the symphysis of an old individual with the following teeth present: Right: I /1 (broken off), I /2 (tip lost), I /3 (root), P /1 (broken), P /2-M /1, M /2 (badly damaged); Left: I /1 (stub), I /2 (root), I /3 (stub), P /1 (roots), P /2, P /3, P /4 (damaged). The only interesting features are the unusually long symphysis, the presence of the broken stub of I /3 instead of the alveolus, as is usually the case, and the unusually strong ridge down the antero-inferior aspect of the symphysis.

This species is represented in the American Museum collections by the badly damaged skull of a very old individual, No. 12389, an exchange from the Carnegie Museum, which was collected from the Lower Titanotherium Beds, West Fork of Corral Draw, Washington County, South Dakota, by Mr. J. B. Hatcher in 1901. This furnishes little new information. There is a trace of the posterior extension of the ectoloph on the left M $3/$, but none on the right side. There is also part of a lower jaw, American Museum No. 9792 (fig. 26), collected by the Expedition of 1902, in the Titanotherium Beds of South Dakota. This includes part of the right ramus with all the cheek teeth and the symphysis with I $1/$ and I $2/$ on each side, as well as the alveolus for I $3/$ on the right side. This lower jaw is certainly conspecific with that (figs. 27 and 28) described and figured by Hatcher (1901). It is an older individual, as all the permanent teeth are in place. The incisor tusks have a sharper lateral ridge than in other specimens of this species. The occlusal relations of this specimen appear to coincide with Lucas' type upper jaw, tending to strengthen its reference to *Trigonias osborni*, along with the young lower jaw described by Hatcher (Carnegie Museum No. 97).

The mounted skeleton of a specimen of *Trigonias* cf. *osborni* is figured by Cockerell (1923).

Individual Variation in *Trigonias osborni*

There are considerable individual differences among the specimens included in this species. Lucas' paratype, U. S. N. M. No. 4815 (fig. 25), has an external valley on P $1/$ between what correspond to the trigonid and the talonid, also seen in an incipient form in Carnegie Museum No. 914a. This is not present in Carnegie Museum No. 97 nor in A. M. N. H. No. 9792 (figs. 27 and 26). A. M. N. H. No. 9792 has an abnormally slender ramus. Carnegie Museum No. 3914a has an unusually long symphysis. I $2/$ usually has a delicate lateral ridge; in A. M. N. H. No. 9792

this ridge is unusually well defined. There is variation as to whether I 3/ or C 1/ is the larger, whether C 1/ is erect or procumbent, in the degree of reduction of the posterior buttress of M 3/, in the length of the diastemas in both upper and lower jaws, in the crown-length of I /2 (largely a function of wear), and in measurements in general. In certain of these characters there is about as much variation between the two sides of the same animal as between two different animals (see tables of measurements). This is also well shown by the position of the mental foramina. In Carnegie Museum No. 97, it is double on the right side beneath the posterior root of P /2 and the anterior root of P /3. On the left side it is single beneath the anterior root of P /2. This is as great a difference as there is between any two different specimens.

All these differences are distributed in no particular order and are purely individual. The animal most different from the group is A. M. N. H. No. 9792, but its individual differences (perhaps partly a matter of sex) do not seem important enough to require any nomenclatural recognition.

Individual Variation in Living Rhinoceroses

The living African black rhinoceros, *Opsiceros bicornis*, furnishes another measure of the large degree of individual variation possible in a given species of rhinoceros. There are, of course, great differences in tooth pattern, according to the degree of wear. It is sometimes not realized that there may still be seven upper cheek teeth on a side, functioning at one time. There is a fine series of about thirty skulls in the American Museum, and among them, seven (Nos. 34743, 14136, 54124, 54283, 27758, 34739, and 54311) retain d P 1/ on one side after all the other permanent cheek teeth are in use. In No. 54311, d P 1/ is retained on both sides, as well as the right d P /1. In several specimens, especially in subadults, the alveolus of d P /1 is still present.

The first deciduous lower premolar is present in most of the calves. In No. 34741, which has M 2/ partly erupted, both d P /1's are present, and small alveoli occur for d I /1 and d I /2, the alveolus for d I /2 being much the larger. The deciduous premolars are retained, except that d P /2 has been lost and P /2 is erupting. In No. 27754, with M 1/1 in place, all d P 1/1's are retained and there is a small alveolus for right d I /2, with left d I /2 just cutting the gum. In No. 27759, a still younger calf, with all the deciduous premolars in place and with the first upper and lower molars just erupting, the alveoli of right d I /1, d I /2, and left d I /1 are present, and left d I /2 is present, barely cutting the gum.

In a calf of *Rhinoceros unicornis*, A. M. N. H. No. 70445, with all the deciduous premolars in place and M 1/1 not yet above the level of the gum, alveoli of left d I /1 and both d I /2's are present, with right d I /1 in place, barely cutting the gum.

All this is another illustration of the amount of individual variation possible, and of the danger of using the presence or absence of a tooth which is in process of being lost, as a definite criterion of specific distinction, still less as a proof of generic distinction.

Professor Osborn has pointed out (verbal communication) the presence of a small roughening of the skin over the frontals, in a specimen of *Rhinoceros unicornis*, A. M. N. H. No. 54456, which would indicate that a very small horn had been present, corresponding in position to the frontal horn of *Opsiceras*. The alternative interpretations of such a condition—parallel mutations in forms with similar genetic constitution, or reversion to an ancestral condition—are obvious. Conversely, Lydekker (1907) mentions the photograph of a fresh-killed full-grown white rhinoceros showing the posterior horn reduced to a scarcely noticeable nubbin, and quotes Selous to the effect that the posterior horn is sometimes a mere lump two or three

inches high. It may be questioned whether the number of horns always has the great phylogenetic significance that is usually attributed to this character.

Trigonias, undescribed species ? near **Trigonias osborni**

A. M. N. H. No. 12308, collected from the Titanotherium Beds, Indian Creek, near the Cheyenne River, South Dakota, by Mr. Albert Thomson in 1904, a jumble of unassociated fragments of various animals, includes the second right upper incisor and the fourth left upper premolar of a member of the genus *Trigonias* (fig. 37). The incisor shows nothing new but the premolar is much more advanced than any specimen of *Trigonias osborni* I have seen; for although it is inside the range in size of specimens of *Trigonias osborni*, the hypocone is a separate, conical cusp, attached to the protocone at the base and separated from the metaconule by a wide deep valley.

This tooth shows just the characters that would lead to the second of the two new species of *Trigonias* described below. It probably represents a valid species but it seems better to leave it to be named from some more complete specimen.

Trigonias wellsi, new species

Pl. 6, figs. 32, 33, Pl. 7, fig. 34.

The holotype is A. M. N. H. No. 13226 (1). This animal is a third larger than *Trigonias osborni*. I 3/?, C 1/?, P 4/?, M 3/?. The canine is larger than the third incisor. None of the upper premolars are anywhere near molariform. The metaloph is incomplete on P 2/. The hypocone on P 2-4/ is merely a bud on the protocone, the two cusps being fully confluent, with an internal notch. The median valley opens widely, posteriorly. A well developed hypostyle is present on P 2/ and P 3/ of both sides, and on left P 4/, but is absent on right P 4/ (fig. 33). The presence of a hypostyle as a free cusp (not as an up-growth of the cingulum), which is otherwise unrecorded among rhinoceroses, living or fossil, bars this species from an-

cestry to any other known form. The pattern of P 1/ is almost obliterated by wear but what is left indicates a pattern identical with the second new species of *Trigonias* described below. A weak internal cingulum is present on all the molars. The ectoloph and metaloph of M 3/ form a straight line. The posterior cingulum of M 3/ is reduced. The post-glenoid and post-tympanic processes are well separated below the external auditory meatus.

This species is founded on a skull, without lower jaw, of an old individual, A. M. N. H. 13226 (1), with which parts of the skeleton are doubtfully associated. This specimen was collected in the Upper Titanotherium Beds, Corral Draw, in the Big Badlands of South Dakota, by Mr. H. F. Wells in 1906, for whom the name is given.

The first and third left incisors, both canines, what is apparently the left deciduous canine abnormally retained to old age, and all the cheek teeth are present. There is also associated a loose first right upper incisor, which may have dropped out of this specimen. If so, it must have done so after death but before fossilization, since the alveolus is filled with completely consolidated matrix. The position and size of the other front teeth are indicated by their alveoli. Since *Trigonias wellsii* is so much larger than *Trigonias osborni* the virtual identity in size of I 1/ is somewhat surprising. The cheek teeth are badly worn but much of the pattern can still be determined. There is an incipient antecrochet on left P 3/. There is nothing very striking about the molars except their large size for so early a form. There is a small, more or less defined tubercle in the valley of M 3/. The roof of the skull is completely lost.

As P 2-4/ of *Trigonias wellsii* are more primitive than the corresponding teeth of *Trigonias osborni*, or even of *Eotrigonias rhinocerinus*, it seems most probable that the

Trigonias line separated from the *Eotrigonias* line before the *E. rhinocerinus* stage, and that the *T. wellsii* line separated from the *Trigonias* stock before the *T. osborni* stage.

***Trigonias gregoryi*, new species**

Figs. 39 and 40

The holotype is A. M. N. H. No. 13226a. This form is almost as large as *Trigonias wellsii*. I 3/?, C 1/?, P 4/?, M 3/?. The upper canine is larger than the third incisor. The pattern of the P 1/'s is similar to that of the paratype of "*Cænopus*" *platycephalus*, figured by Osborn (1898, Pl. XIII, fig. 9). Upper premolars 2-4 are very progressive for *Trigonias*, bearing more resemblance to "*Cænopus*" *platycephalus* than to either of the other two species of *Trigonias*, or to any other hitherto known form. There is no hypostyle on the upper premolars. P 2/ is virtually molariform, with a complete metaloph which is separate from the protoloph down to the level of the cingulum. P 3/ and P 4/ are also progressive, although less advanced than P 2/. The hypocone of P 3/ is nearly independent of the protocone but is not completely joined to the metaconule. It is more advanced in both respects, however, than either *Trigonias wellsii* or *Trigonias osborni*. The metaloph is almost complete on the right P 4/ but much less so on the left P 4/, where the hypocone is rudimentary. There is what appears to be an antecrochet on the right P 4/. This is an unprecedentedly early appearance for this structure. The molars have no internal cingulum. The ectoloph and metaloph of M 3/ form a straight line. The posterior cingulum of M 3/ is well developed. The posterior margin of the nasal incision is vertically above the anterior border of P 2/.

This species is founded on the skull of a young adult, A. M. N. H. No. 13226a, without the lower jaw, with doubtfully associated parts of the skeleton, which was collected in 1906 by Mr. H. F. Wells from the Upper Titanotherium Beds, Corral Draw, Big Badlands, South Dakota. The spe-

cific name is given in recognition of Professor William K. Gregory. The left canine, all the cheek teeth, and the alveoli of the other front teeth, are present. The rear half of the skull is badly mutilated, especially on the right side, where it is largely missing. There is nothing striking about the molars except their large size for a lower Oligocene true rhinoceros. There is a very poorly defined tubercle in the valley of M 3/. The cheek teeth are in somewhat the same stage of evolution as those of "*Leptacera-therium*" *trigonodum*. They are, however, very much larger, and P 1/, P 3/, and P 4/ are less advanced toward the molar pattern.

Trigonias gregoryi, especially in the progressiveness of P 2/, tends to break down the clear distinction between *Trigonias* and the later forms, usually referred to *Cænopus*, as this name was used by Troxell (1921a). In the totality of its characters, however, it resembles *Trigonias* more than any of the later forms. The presence of this intergrading form certainly is no reason for abandoning the otherwise valid genus *Trigonias*—unless for a believer in special creation.

Trigonias gregoryi ? Wood Pl. 6, fig. 38.

I ?/3, C ?/0, P ?/4, M ?/3. The erupting permanent incisor tusks resemble those of the later Oligocene rhinoceroses in being ridged on the median side only, as in some specimens of *Trigonias osborni*, rather than the other specimens with external ridges as well. I /2 procumbent. P /3 and d P /4 are molariform, P /2 nearly so. P /2 resembles P /3 more than it does P /1. P /1 is nearly as advanced as P /2 of *Trigonias osborni*. P /2 and P /3 are much further metamorphosed than the corresponding teeth of *Trigonias osborni*. The basal cingulum of P /2 and P /3 surrounds the posterior crescent, both behind and internal to it, lapping over on the metaconid.

This description is based on a complete lower jaw, 13226 b, of a young individual, collected from the Upper

Titanotherium—Beds in Corral Draw, Big Badlands, South Dakota, by Mr. H. F. Wells in 1906. The first and third incisors are represented by alveoli only, the permanent second incisors are partly erupted, the first premolars are in place, the second and third permanent premolars are erupting, the greatly worn fourth deciduous premolars are still in place, the first and second molars are in place and the erupting third molars are still well below the level of the gum.

This form is too large and too progressive to be referred to *Trigonias osborni*. It is difficult to refer it with any assurance to either *Trigonias wellsi* or *Trigonias gregoryi*. It is also possible, though not at all likely, that it represents still a third species. The mode of fossilization is the same as the type of *Trigonias gregoryi* and it was regarded by the collector as the lower jaw belonging with the skull. It cannot be the same individual, however, as shown by the occlusal relations and especially by the considerable wear of the upper molars of the type of *Trigonias gregoryi*, since M /1 and M /2 of this lower jaw are absolutely unworn. Judging from the occlusal relations of the first and second molars, this individual when fully grown would have been appreciably larger than the type of *Trigonias gregoryi* and, apparently, slightly larger than the type of *Trigonias wellsi*. It would, however, have been well inside the probable range of variation in size of either species, even using the narrow limits of specific variability permitted by modern systematic zoologists.

I assign it provisionally to *Trigonias gregoryi*, since the premolars show more advance over those of *Trigonias osborni* than would be expected in the lower premolars of *Trigonias wellsi*, judging by the stage of evolution of the upper premolars of *Trigonias wellsi*.

Perhaps associated with this lower jaw there is a left first upper incisor with enough of the premaxillary bone adherent to prove that it was part of still a third skull.

The tooth is somewhat damaged. The measurements are as follows:

Crown length	13.0 mm.
Antero-posterior	18.0 mm.
Transverse	10.5 mm.

The American Museum specimens which have just been described as *Trigonias wellsi*, *Trigonias gregoryi*, and *Trigonias gregoryi*?, are all parts of an associated find, including parts of at least five individuals, from the Upper Titanotherium Beds, according to the original correspondence of the collector, Mr. H. F. Wells. They were provisionally catalogued as two skulls and a large part of the skeletons of a new species of ? *Trigonias*.

***Trigonias paucidens*, new species**

Pl. 6, fig. 35, Pl. 7, fig. 36.

The holotype is A. M. N. H. No. 11865, a skull without the lower jaw, from the Lower Titanotherium Beds of Quinn Draw, Big Badlands, South Dakota, collected by Mr. H. F. Wells in 1903. It was provisionally catalogued as *Cænopus platycephalus*, and has only now been sufficiently prepared and reinforced to be available for study. The skull belonged to a fairly old individual, since the pattern is nearly obliterated on P 1/–P 3/ and on M 1/.

I 3/?, C 0/?, P 4/?, M 3/?. The skull is a shade larger than any measured specimen of *Trigonias osborni*. It is appreciably smaller than the other species of *Trigonias*, or than "*Cænopus*" *platycephalus*. I 2/ is larger than I 3/. None of the cheek teeth has an external cingulum. The pattern of P 1/–P 3/ is nearly obliterated by wear, but it must have been much like *Trigonias osborni*. There is a strong internal cingulum on P 2/–P 4/. The pattern of P 4/ is indistinguishable from that of *Trigonias osborni*. The upper molars have no internal cingulum, except a trace across the median valleys of M 1/ and M 2/. M 3/ is inside the range of variation of *T. osborni*, having a very faint trace of a posterior buttress and a well-developed post-fossette.

Right I 1/ and left I 1/ and I 2/ are represented by their alveoli, only. These teeth presumably dropped out after the death of the animal. Left P 3/ and P 4/ are also missing, but were almost certainly lost during life, as there was apparently some deposition of bone in their alveoli. Right P 4/, left M 2/ and left M 3/ each have a slight pit at some point on the occlusal surface, which may, perhaps, be due to caries.

On the basis of the loss of C 1/, there would be precedent for erecting this species into a new genus. However, there does not seem to be any necessity for such a step. Except for the lost tooth, it could easily be included in *Trigonias osborni*. If I 3/ instead of C 1/ is the missing tooth, it would seem to approach the definition of *Leptaceratherium*; but, actually, it has little in common with "*Leptaceratherium*" *trigonodum*. However, the missing tooth is almost certainly the canine. Although the premaxillary suture abuts against the middle of the lateral front tooth, nevertheless this tooth appears, actually, to be set in the premaxillary. Additional confirmation is furnished, by the fact that, in other species of *Trigonias*, this suture runs well anterior to the canine, sometimes coming in contact with I 3/, and by the presence, in the type of *Trigonias paucidens*, of slight pits which may have held the deciduous canines, well behind the last front tooth. Detailed measurements are given below.

Trigonias paucidens was probably very close to the ancestor of "*Cænopus*" *platycephalus*, if not actually ancestral to it. Troxell's suggestion (1921a) that "*Leptaceratherium*" *trigonodum* was ancestral to "*Cænopus*" *platycephalus* seems, at the least, highly improbable, since the former species has lost the first lower premolar (A. M. N. H. Nos. 529 and 1489), which is typically retained in the latter (A. M. N. H. Nos. 542 and 545). The fact that P 3/ of "*Leptaceratherium*" *trigonodum* is so much more progressive than P 3/ of "*Cænopus*" *platycephalus* is an objection of still greater weight. On the other hand, *Tri-*

gonias paucidens fulfills all the necessary requirements for the ancestor of "*Cænopus*" *platycephalus*.

Trigonias cf. **osborni** Lucas, or cf. **Trigonias paucidens** Wood.

Caenopus platycephalus nanolophus Troxell. Troxell, 1921a

The holotype, Yale Peabody Museum No. 12489, was collected from the Oligocene of Colorado by Mr. Deven-dorf. The type consists of right P 1/ and left P 1/-M 3/. Its geological level seems to be entirely uncertain, beyond being Oligocene. It falls right into place as a specimen of *Trigonias osborni*, or, perhaps, *Trigonias paucidens*. It agrees with the other specimens of *Trigonias osborni*, not only in detailed measurements, but in almost every other character. (This resemblance is only partly shown by a comparison of Troxell's figure with mine.) The most striking common characters are the very deep valley, opening posteriorly on P 3/ and P 4/, which is found in all but the most worn specimens of *Trigonias osborni*, and the union of protocone and hypocone on P 2/, although they are separated internally by a deep groove. I am unable to regard the few characters in which it differs from other specimens of *Trigonias osborni* as making it worthy of specific or subspecific distinction. These characters are: the slightly greater length of the molars, especially M 1/, and the fact that the protoloph of P 1/ is nearly perpendicular to the ectoloph, instead of swinging well posteriorly as in the holotype (U. S. N. M. No. 3924). This specimen (Y. P. M. No. 12489) shows just the characters needed for an ancestor of *Trigonias gregoryi*.

Troxell recognized the fact that this form was very different from any other well known form. The unsatisfactory character of the published figures of *Trigonias osborni*, together with the highly dubious assignment of Y. P. M. No. 12489 to the Middle or Upper Oligocene, prevented him from recognizing its closest relationships. The only published figures of the cheek teeth of *Trigonias* were the very badly worn specimens in Hatcher's paper, which

suggest slight resemblance to the little-worn teeth of the Yale specimen. And, of course, "*Cænopus*" *platycephalus* has retained much of its heritage from the *Trigonias* stage. This specimen is more probably referable to *Trigonias osborni* than to *Trigonias paucidens*, in view of the fact that the former species is much better represented, numerically, in the collections. However, strictly speaking, the species is indeterminate, due to the absence of the front teeth, which furnish the only real distinguishing character between *Trigonias osborni* and *Trigonias paucidens*.

Troxell's figure and description are very complete, and furnish a valuable reference specimen—the first not badly worn—for *Trigonias osborni*. The figure is misleading to the extent that there is no posterior hook on the hypcone of P 2/ of the specimen.

An unworn right P 4/ in the Yale Museum, No. 12562, is unquestionably the same form.

In the tables that follow, certain measurements given by Lucas or Hatcher are omitted. The "greatest length of the premaxillaries" is often hard to determine, due to the difficulty in distinguishing sutures from cracks. The "crown length" of I 1/ or I 2/ is valueless, since it is dependent on the amount of wear. In various cases measurements are not given when the specimen is so badly damaged or distorted that figures would be valueless or misleading.

The American true rhinoceroses of the middle and upper Oligocene, formerly referred to *Aceratherium* Kaup, 1832, are now usually referred to *Cænopus* Cope, 1880 (Genoholotype, *Aceratherium mite*). If these rhinoceroses are regarded as a single genus, the name *Subhyracodon* Brandt, 1878 (originally including *Aceratherium mite*, *Aceratherium occidentale* and *Aceratherium quadriplacatum*) must hold for all of them. Matthew implies this (Osborn and Matthew, 1909, and Cope and Matthew, 1915) but does not make the statement explicitly. As *Aceratherium quadriplacatum* was made the type of *Anchisodon*

[illegible]

Table IIIB

	Trigonias osborni Holotype U.S.N.M. 3924			Trigonias osborni C.M. 96 (95)			Trigonias osborni C.M. 96			Trigonias sp. indesc.? A.M.N.H. 12308			Trigonias weilsi A.M.N.H. 13226			Trigonias paucidentis Holotype A.M.N.H. 11865			Trigonias "nanolophus" Holotype Y.P.M. 12439			Trigonias "nanolophus" Y.M.P. 12562		
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
m Length of p ³	25	20	---	27	26	22	22	22	27.5	30	29	29.5	23	---	28.5	28.5	---	---	---	---	---	---	---	---
a Width, p ³	40	33	---	39	35.5	35	35	35	47	46.5	45	44.5	36	---	34	34	---	---	---	---	---	---	---	---
Index, p ³	62.5	60.6	---	71.5	70.1	62.9	62.9	62.9	58.5	65.2	64.4	66.3	65.9	---	77.9	77.9	---	---	---	---	---	---	---	---
m Length, p ⁴	---	24.5	21.5	25	26.5	25	25	25	32.5	32	32	31	26	---	27	27	---	---	---	---	---	---	---	---
a Width, p ⁴	---	36	37.5	40	39.5	39	39	39	52	53.5	50	50	40.5	---	39	40	---	---	---	---	---	---	---	---
Index, p ⁴	---	64.5	57.5	62.5	67.0	64.1	64.1	66.7	62.5	59.6	64.0	62.0	64.2	---	69.2	62.5	---	---	---	---	---	---	---	---
m Length, m ¹	---	28.5	26	32	34	33	32	32	43	43	43.5	44	32.5	34	37	38	---	---	---	---	---	---	---	---
a Width, m ¹	---	43	41.5	46	45	41	42	42	55	56	55.5	55	44.5	45	45	45	---	---	---	---	---	---	---	---
Index, m ¹	---	66.5	62.7	71.1	70.1	60.5	70.2	70.2	78.2	78.2	78.4	80.0	73.0	79.1	86.0	86.4	---	---	---	---	---	---	---	---
m Length, m ²	---	37.5	34.5	39	39	36	---	---	49.5	48.5	48	48	41.5	41	40	42	---	---	---	---	---	---	---	---
a Width, m ²	---	44.5	46	46.5	47	48	---	---	61	61	63	63	49	49	48	47.6	---	---	---	---	---	---	---	---
Index, m ²	---	84.5	75.0	85.9	84.9	75.0	---	---	81.1	79.6	76.2	76.2	84.3	83.7	85.5	88.4	---	---	---	---	---	---	---	---
m Length, m ³	---	38	38	39	38.5	36.5	34.5	34.5	50	51	49.5	50.5	41	39	---	---	---	---	---	---	---	---	---	---
a Width, m ³	---	42.5	42.5	43	43	45	44	44	59	58	60	60.5	45.5	46.5	---	---	---	---	---	---	---	---	---	---
Index, m ³	---	89.4	89.4	89.4	89.8	81.1	78.4	78.4	84.7	87.9	82.5	83.6	90.1	83.9	---	93.0	---	---	---	---	---	---	---	---
Pax to ob. conyle	---	[diorted] [512 536]		---	---	---	---	---	596	596	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Width across zygoma	---	[crushed] [187]		245	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Depth incision ant. nares	---	142	134	---	---	---	---	---	---	---	127	153.6	133	---	---	---	---	---	---	---	---	---	---	---
Height occiput above oc. conyle	90+	---	155.8	160	145	141	---	---	---	---	---	---	140	140	---	---	---	---	---	---	---	---	---	---
Width bet. p ¹ & p ²	---	[36.5] [badly crushed] [36.5]		51	---	---	---	---	83	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	85.5	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---

a, greatest width of
d, deciduous
e, estimated
g, greatest
m, middle axis
p, permanent
s, as set in plaster
v, alveoli only

	Trigonias obornii			Trigonias obornii			Trigonias obornii			Trigonias obornii			Trigonias obornii			Trigonias obornii		
	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L
Tip of I_2 to back of I_3	52	52	54.5	53	---	---	43.5	---	---	---	---	---	---	---	---	---	---	---
Crown length of I_1 (from root)	---	---	9.5	10	---	---	14.5	---	---	---	---	---	---	---	---	---	---	---
$\frac{1}{2}$ A-P diam. I_1 at root	8	9	8	8	8.5	8	6	7.5	---	---	---	---	---	---	---	---	---	---
$\frac{1}{2}$ Tr. diam. I_1 at root	7	7	8	8	7	7	7	---	---	---	---	---	---	---	---	---	---	---
$\frac{1}{2}$ A-P diam. I_2	12	13	13	13.5	14.5	14.5	11	11.5	11+	14+	---	---	---	---	---	---	---	---
$\frac{1}{2}$ Tr. diam. I_2	16	17	19	20	20.5	19	16	16	16.5+	17.5+	---	---	---	---	---	---	---	---
Crown-length I_3 from root	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
A-P diam. I_3 at root	8	7	---	---	7	5	---	---	7	---	---	---	---	---	---	---	---	---
Tr. diam. I_3 at root	7	7	4	5	5	4	---	---	6	---	---	---	---	---	---	---	---	---
Diastema	36	36	35	29	27	34	26.5	---	40	40	---	---	---	---	---	---	---	---
$P_1 - M_3$	---	---	210	217	210	---	202	---	270	263	---	---	---	---	---	---	---	---
$P_2 - M_5$	---	---	197	197	191	---	188.5	---	249	252	---	---	---	---	---	---	---	---
$P_1 - A$	---	---	90	97	94.5	89	86	84	---	122.5	112.5	---	---	---	---	---	---	---
$P_2 - A$	---	---	75	79.5	78	71	75.5	71	---	103	103	---	---	---	---	---	---	---
$M_1 - M_3$	---	---	122	117	117	---	118.5	---	167	160	---	---	---	---	---	---	---	---
$\frac{1}{2}$ Length, P_1	---	---	18	17	17	---	13.5	---	21	20.5	---	---	---	---	---	---	---	---
$\frac{1}{2}$ Width, P_1	---	---	10	8	8	---	8	---	11.5	11	---	---	---	---	---	---	---	---
Index, P_1	---	---	180.0	212.5	212.5	---	168.8	---	182.6	186.4	---	---	---	---	---	---	---	---
$\frac{1}{2}$ Length, P_2	---	---	24	24	22.5	21	22	18.5	---	31	31	---	---	---	---	---	---	---
$\frac{1}{2}$ Width, P_2	---	---	16.5	16	15	16.5	16.5	13	---	20	20	---	---	---	---	---	---	---
Index, P_2	---	---	133.3	150.0	150.0	127.3	141.9	142.5	---	155.0	155.0	---	---	---	---	---	---	---
a, deciduous e, estimated g, greatest m, middle axis For lower cheek teeth the width is taken across the talonid.																		

Cope, 1879, and in any case is merely a synonym for *Aceratherium occidentale*?, given to the milk teeth, and as *Aceratherium mite* was later made the type of *Cænopus*, *Aceratherium occidentale* becomes the genolectotype of *Subhyracodon*, fixed by elimination (Cope and Matthew, 1915). As a descriptive name *Subhyracodon* is seriously misleading; unfortunately there can be no question of its validity.

I shall try to show that this group splits naturally into three rather widely separated series, which would seem to deserve subgeneric or generic rank. As they appear to be distinct through most of the Oligocene and as only the largest line can be traced with any great probability to any known member of the genus *Trigonias*, they are here ranked as distinct genera. This has the incidental merit of simplifying the nomenclature, reducing the scope of the name *Subhyracodon*, and keeping the historic name *Cænopus* from being relegated into the synonymy.

Caenopus Cope, 1880

Genoholotype: *Aceratherium mite* Cope, 1875.

Questionably referred species: *Cænopus* ? *dakotensis* Peterson, 1920. *Cænopus* ?? *minor* (Filhol) 1884.

Small, North American and European ?, Oligocene rhinoceroses; heavier but no taller than *Hyrachyus eximius* Leidy; I 2/2, C 0?/0, P 4/3, M 3/3; P 2/ and P 4/ have the metaloph definitely separated from, and parallel with, the protoloph; P 3/ is less advanced. The very progressive character of P 4/ is the most striking character. A very weak and interrupted internal cingulum is present on the upper molars. Manus tridactyl?

This genus may be ancestral to *Menaceras* (= *Diceratherium*) *cooki* (Peterson). The possible inclusion of one or more European forms inside the limits of this genus is an interesting question which should be left open for the present.

"*Cænopus*" *persistens* Osborn is probably referable to *Diceratherium*.

It is possible that the European genus *Præaceratherium* Abel is congeneric with *Cænopus*. The teeth of *Præaceratherium minus* (Filhol), figured by Abel (1910), are almost exactly identical with those in the maxilla of *Cænopus mitis* in size and are strikingly similar in character. P 4/ is molariform and P 2/ is more advanced than P 3/. An extensive synonymy is given by Abel. The specimen referred by Koch to *Præaceratherium minus* is more suggestive of *Subhyracodon* cf. *occidentale* (Koch, 1911; Abel, 1914).

***Caenopus mitis* (Cope), 1875**

Fig. 36, Osborn, 1898

Aceratherium mite Cope. Cope, 1875.

Aceratherium (*Subhyracodon*) *mite* (Cope). Brandt, 1878.

Cænopus mitis (Cope). Cope, 1880.

Aceratherium pumilum Cope. Cope, 1885 (name only).

Cænopus pumilis Cope. Cope, 1891.

Aceratherium mite Cope. Osborn, 1898.

Cænopus mitis (Cope). Osborn and Matthew, 1909.

Cænopus (= *Subhyracodon*) *mitis* (Cope). Cope and Matthew, 1915.

Cænopus mitis (Cope). Troxell, 1921 a.

The holotype is a mandible, A. M. N. H. No. 6325. The paratype, a badly damaged set of upper cheek teeth, A. M. N. H. No. 6325, is probably associated with the type. Mixed with these specimens there are also some upper teeth, A. M. N. H. No. 6326, formerly regarded as a paratype but here referred to *Subhyracodon copei*. Associated with these specimens there are parts of a left premaxillary with the anterior tip of the maxillary attached, which shows the alveoli, a right femur and astragalus, a left radius and tibia, an axis and various other vertebræ, as well as fragments. These specimens were collected by Professor Cope in 1873 for the Hayden Survey from the Upper Titanotherium Beds of Cedar Creek, Logan Co., Colorado. I 2/?, C 1-0/?, P 4/3, M 3/3. The alveolus for the upper canine is very small. P 2/ is molariform with separate parallel lophs. The hypocone of P 3/ is connected about equally closely to the protoloph and the metaloph. P 4/ has

a clearly separated metaloph, partly connected with the protoloph by a spur near the internal margin. If continued all the way across the valley, this spur would become what Troxell has named the "mure." Phylogenetically, the mure is probably merely the reduced isthmus between the protocone and hypocone. The upper molars have no cristæ and very weak internal cingula. I /2 is semiprocumbent.

The doubtfully associated foot bones are figured by Cope and Matthew (1915, Pl. CIV and CV). Measurements are given by Cope (1875). The number of toes in the manus is not definitely known. A carpus in the Princeton Museum referred, perhaps incorrectly, to this species, has an undivided distal facet on the unciform (Wortman, 1893). Osborn and Scott regarded this carpus as probably tridactyl but Wortman considered the evidence inconclusive. The reference is uncertain, as *Subhyracodon copei* occurs in the same beds and is about the same size. The latter was in all probability tridactyl. Until, therefore, a manus and skull of *Cænopus mitis* are found certainly associated, the question must be left open.

Cænopus ? dakotensis Peterson, 1920 Fig. 39, Osborn, 1898

Aceratherium mite ? Cope. Osborn, 1898.

Cænopus dakotensis ? Peterson. Peterson, 1920.

Cænopus tridactylus (Osborn). Troxell, 1921 a.

The holotype is A. M. N. H. No. 1110, collected from the Protoceras Beds, near the Cheyenne River, S. D., by the American Museum Expedition of 1894.

I /2, C /0, P /3, M /3. I /2 is semiprocumbent.

By a lapsus calami Troxell (1921 a) calls *Cænopus dakotensis* Peterson a synonym of *Cænopus tridactylus* (Osborn). As Peterson (1920) explains, *Cænopus dakotensis* is a provisional name, given largely on stratigraphic grounds, to the lower jaw of an animal even smaller than the type of *Cænopus mitis*. It was described and figured by Osborn (1898). Detailed measurements are given below.

Menoceras Troxell, 1921

This genus is doubtfully distinct from *Diceratherium* Marsh. If it be regarded as the end-product of a distinct line of evolution, as yet largely unknown, the separation seems warranted. The structural differences, however, are hardly worthy of generic rank—certainly not if it is a descendant of *Subhyracodon tridactylum*. The more individual characters of *Menoceras cooki* are: relatively small size, knob-shaped horn cores at the tip of the nasals (as opposed to the long narrow horn of the larger forms; little tendency for a mure to develop on the upper premolars; enlargement of the crista of d P 2/ into a full-sized transverse crest; pattern of the upper cheek teeth extremely complicated; animal much more specialized for cursorial life than *Subhyracodon tridactylum*, and therefore, probably, than the large diceratheres. (See table of limb ratios below.)

Menoceras cooki (Peterson) 1906

Pl. LX, Peterson, 1920

Diceratherium cooki Peterson. Peterson, 1906.*Diceratherium arrikarens* Barbour. Barbour, 1906.*Diceratherium schiffi* Loomis. Loomis, 1908.*Diceratherium aberrans* Loomis. Loomis, 1908.*Aceratherium stigeri* Loomis. Loomis, 1908.*Diceratherium loomisi* Cook. Cook, 1912.*Diceratherium cooki* Peterson. Peterson, 1920.*Menoceras cooki* (Peterson). Troxell, 1921 b.

Genoholotype: Carnegie Museum No. 1572. Horizon: Upper Harrison. Locality: Nebraska. I 2/2, C 0/0, P 4/3, M 3/3. I /2 erect to semi-erect.

This species has been monographed by Peterson (1920) and made the type of the genus *Menoceras* by Troxell (1921 b). The further splitting off of *Metacænopus* Cook from *Diceratherium* seems totally unjustifiable.

It seems possible that *Menoceras cooki* is derived from *Cænopus* ? *dakotensis* as suggested by Peterson (1906 and 1920), or from *Cænopus mitis*. At least other possibilities seem less likely. The much smaller size is a considerable

difficulty in the way of deriving it from *Subhyracodon tridactylum*.

In a specimen of *Menoceras cooki* in the American Museum, Field number 9, expedition of 1914, the first deciduous right lower premolar is retained after all the permanent cheek teeth have come into use. It is very small.

The crista of d P 2/, as pointed out by Peterson, is elongated into an independent transverse crest, almost as long as the protoloph or metaloph. This tooth shows more specialization over the corresponding tooth in *Subhyracodon* than any other tooth, deciduous or permanent. No correlated specialization occurs in d P /2.

Subhyracodon Brandt, 1878

The genoholotype (fixed in Cope and Matthew, 1915, by elimination) is *Aceratherium occidentale* (Leidy). (The genotypes, as given by Brandt, are *Aceratherium mite*, *Aceratherium occidentale*, and *Aceratherium quadriplacatum*. See above.) These are moderate sized North American Oligocene rhinoceroses, which merge into *Diceratherium*, developing paired horns on the nasals in the male. The manus is tridactyl. I 2/2, C (1)–0/0, P 4/(4)–3, M 3/3. I 3/ is the first upper tooth to be lost in this series, as distinct from the larger series, in which C 1/ is the first upper tooth to be lost. P 2/ is molariform. P 3/ and, later, P 4/ become progressively molariform. The internal cingulum on the premolars is complete and prominent. There is a well-developed internal cingulum on the upper molars, which is usually more or less interrupted. I /2 is semi-erect to procumbent.

Referred species: *Subhyracodon trigonodum* (Osborn and Wortman), *Subhyracodon copei* (Osborn), *Subhyracodon metalophum* (Troxell), *Subhyracodon tridactylum* Osborn.

Leptaceratherium Osborn, 1898

The genoholotype is *Aceratherium trigonodum* Osborn

and Wortman, 1894. I 2/2, C 1-0/0, P 4/3, M 3/3. I /2 is semi-procumbent to procumbent.

This generic name is here placed in synonymy with *Subhyracodon*. The upper premolar pattern is not very different from that of more typical members of the genus, although it is somewhat more primitive, and the exact degree of reduction of the upper canine is certainly not a character of generic importance.

Meninatherium Abel may be congeneric with *Subhyracodon*.

***Subhyracodon trigonodum* (Osborn and Wortman)**

Fig. 46 c, Osborn, 1898

Aceratherium trigonodum Osborn and Wortman. Osborn and Wortman, 1894.

Aceratherium (Cænopus) mite Cope. (A. M. N. H. No. 521.) Osborn and Wortman, 1894.

Leptaceratherium trigonodum (Osborn and Wortman). Osborn, 1898.

Aceratherium copei Osborn (paratype, A. M. N. H. No. 521). Osborn, 1898.

Leptaceratherium trigonodum (Osborn and Wortman). Osborn and Matthew, 1909.

Cænopus (Leptaceratherium) trigonodus (Osborn and Wortman). Troxell, 1921 a.

The holotype is A. M. N. H. No. 528, from the Upper Titanotherium Beds of South Dakota, collected by the Expedition of 1892. Range: Upper Titanotherium Beds to Lower Oreodon Beds.

Slightly larger than *Subhyracodon copei* or *Cænopus mitis*, slightly smaller than *Subhyracodon occidentale*. I 2/2, C 1-0/0, P 4/(4)-3, M 3/3. P 2/ is fully molari-form with the lophs united well above the cingulum. In both P 3/ and P 4/ the hypocone is very slightly developed as a distinct cusp. In P 3/, when even slightly worn, the protoloph and metaloph are connected like a blunted v, inclosing a deep basin. I /2 is semiprocumbent to procumbent.

An unworn specimen such as the type is very easily recognized, as the small and poorly defined hypocone of

P 3/ and P 4/ is united firmly to the metaconule but separated by a slight constriction from the protocone.

In P 3/ the metaconule is attached to the posterior edge of the hypocore instead of the anterior edge as in *S. copei* and *S. occidentale*. In P 4/ the median valley would always escape internally, never posteriorly as in *S. copei* and *S. occidentale*, until the tooth was sufficiently worn so that the valley was completely enclosed.

There is additional confirmation of Osborn's discovery (1898) that *Subhyracodon trigonodum* retained the upper canine into maturity. The partly prepared skull of a very old individual from the Lower Oreodon Beds (A. M. N. H. No. 9790) probably referable to this species, has well marked alveoli for right I 1/, I 2/, and C 1/. The transfer of the paratype of *Subhyracodon copei* (A. M. N. H. No. 521), which has a superior canine, to this species, is still further confirmation. That this transfer is necessary can be seen by comparing P 3/ of No. 521 with the types of the other two species. (See Osborn, 1898, fig. 448.)

A. M. N. H. No. 1131, probably referable to this species, has on both third upper molars a very slight trace of the posterior extension of the ectoloph, with a fairly distinctly defined post-fossette.

U. S. N. M. No. 8430 should be referred to this species. L P /1 (probably Ld P /1) and the roots of the corresponding tooth on the opposite side are retained. The connection between the protoloph and metaloph of P 2/ is carried unusually high for this species. This is a young specimen with all the deciduous fourth premolars still in place and with the third upper molars just cutting the gums. P /3 is almost molariform, P /2 is definitely premolariform.

Subhyracodon copei (Osborn) 1898

Fig. 44 A, Osborn, 1898

Aceratherium (Cænopus) mite Cope. (A. M. N. H. No. 522.) Osborn and Wortman, 1894.

Aceratherium copei Osborn. Osborn, 1898 (A. M. N. H. No. 522).

Cænopus (= *Subhyracodon*) *copei* (Osborn). Osborn and Matthew, 1909.

Cænopus copei (Osborn). Peterson, 1920.

Cænopus copei (Osborn) in part. Troxell, 1921 a.

The holotype is A. M. N. H. No. 522 from the Lower Oreodon Beds of South Dakota, collected by the Expedition of 1892. I 2/?, C 1/?, P 4/?, M 3/?. This species is smaller than *Subhyracodon trigonodum* or *Subhyracodon occidentale*. This shows most clearly in the molar series, which is shorter by about a sixth. P 3/ is also much more primitive than in either of the other species. P 2/ is molariform, P 3/ and P 4/ are still unmetamorphosed. The protoloph and metaloph of P 2/ are united well above the cingulum. In P 3/, well into maturity, the hypocone is not attached to the metaconule, letting the median valley escape posteriorly. P 4/ resembles *Subhyracodon occidentale* in shape more closely than it does *Subhyracodon trigonodum*. It is slightly more advanced than P 3/, so that, in the type specimen, the posterior outlet of the valley is already closed.

The "paratype" of *Cænopus mitis*, A. M. N. H. No. 6325, should be referred to this species.

The "paratype" of *Subhyracodon copei*, A. M. N. H. No. 521, should be referred to *Subhyracodon trigonodum*. Comparison of Osborn's figures (1898, p. 147) suggests this strongly, and on comparison of the specimens this change is virtually necessitated by the character of P 3/, which has the enclosed basin characteristic of P 3/ and P 4/ in *Subhyracodon trigonodum*. As the specimen is young, still retaining d P 4/, the characters of this tooth cannot be used as an additional check.

The failure to refer these two paratypes to their correct species is in large part the cause of the general confusion as to the characters of these species. This has been particularly the case with *Subhyracodon copei* and *Subhyracodon occidentale*. Besides the obvious difference in size and the retention of the upper canine, there is a marked differ-

ence in P 3/. "Third and fourth upper premolars with tetartocone spurs united chiefly with protoloph"—(Osborn, 1898). In *Subhyracodon occidentale*, on the other hand, P 3/ has its protoloph and metaloph approximately parallel and partly separate, with an internal outlet for the median valley. *Subhyracodon copei* differs from *Subhyracodon trigonodum* in the pattern of both P 3/ and P 4/, where the outlet of the valley is median.

There are two specimens referred to *Subhyracodon copei*, A. M. N. H. Nos. 6326 and 12452, from the Upper Titanotherium Beds.

The closest relationships of *Subhyracodon copei* are with *Subhyracodon occidentale*, to which, as Osborn has pointed out (1898), it is in all probability ancestral. Increase in size, earlier loss of C 1/ and a slight advance in P 3/ are the chief advances necessary to give the later form.

***Subhyracodon occidentale* (Leidy) 1854** Pl. XII, Leidy, 1854 a

Rhinoceros occidentalis Leidy. Leidy, 1850. Proc. Phil. Acad. Nat. Sci., V, p. 119. This is a nomen nudum, as the type is lost and would, in any case, be indeterminable.

Rhinoceros occidentalis Leidy. Leidy, 1854 a.

Aceratherium occidentale (Leidy). Leidy, 1854 b.

Aceratherium (Subhyracodon) occidentale (Leidy). Brandt, 1878.

Aceratherium occidentale (Leidy). Cope, 1879 a.

Aceratherium occidentale (Leidy). Osborn, 1898.

Cænopus occidentalis (Leidy). Osborn, 1900.

Cænopus (= Subhyracodon) occidentalis (Leidy). Osborn and Matthew, 1909.

Cænopus trigonodus allus Troxell. Troxell, 1921 a.

Cænopus copei Troxell (not Osborn) in part. Troxell, 1921 a.

Aceratherium occidentale (Leidy). Osborn, 1923 a.

I agree with Osborn (1898) and Sinclair (1924) that *S. occidentale* is valid, in preference to Troxell's opinion (1921) that it should be abandoned in favor of *S. copei*.

The neotype is U. S. National Museum No. 114. The range of this species is probably the Lower and Middle Oreadon Beds. This animal was slightly larger in nearly all dimensions than *Subhyracodon copei*. The molar series

is markedly longer than in *Subhyracodon copei*. The pre-molar series is distinctly shorter than in *Subhyracodon metalophum* and less advanced (especially P 4/). Its inferiority in size as compared with *Subhyracodon tridactylum* is still more apparent.

There are no traces of horn cores. The manus is tri-dactyl. I 2/2, C 0/0, P 4/3, M 3/3. d I 2/2, d C 0/0, d P 4/4. I 2/ is still large. P 2/ has parallel, separate lophs. P 3/ has its protoloph and metaloph fully confluent after slight wear but the hypocone is better developed than in *Subhyracodon trigonodum* and, unlike *S. copei*, the outlet of the valley is median. The metaconule of P 4/ usually turns anteriorly and abuts against the outer side of the hypocone, which is only partly distinct from the protocone. The median valley usually escapes posteriorly (much like P 3/ of *Subhyracodon copei*) until a moderately advanced stage of wear. I /2 is semi-erect.

The character of P 4/ before excessive wear is well shown in A. M. N. H. No. 6330, collected by Cope in Colorado in 1873, in the White River Beds. These teeth show clearly the original pattern of the type specimen before it was greatly worn. (See Pl. XII, Leidy, 1854 a.) It is also well shown in A. M. N. H. No. 1113, collected by the A. M. N. H. Expedition of 1894, from the "Turtle-Oreodon Layer," Oreodon Beds, Cheyenne River, South Dakota, a specimen younger than the type of *Subhyracodon copei*, about the age of the type of *Subhyracodon trigonodum*, for M 3/ is not quite fully erupted. P 3/ has its metaloph already complete, united to the protoloph and completely enclosing the median valley. P 4/, very slightly worn, shows a posterior outlet for the median valley between the hypocone and the metaconule.

The specimen which Koch (figured by Koch, 1911 and Abel, 1914) referred to *Præaceratherium minus* seems distinct from the type. On the other hand, both in size and dental characters, it seems so like *Subhyracodon occidentale*, that if it had been found in North America, it would

have been referred to that species.

***Subhyracodon occidentale* (Leidy)**

Cænopus trigonodus allus Troxell. Troxell, 1921 a (figs. 1 and 2).

The holotype is Y. P. M. No. 12052, from the Oreodon Beds of Nebraska, collected by Mr. H. C. Clifford. This is a young individual. The third right upper molar was just about to erupt, as were both third lower molars.

I fail to see any marked resemblance between this specimen and the type of *Subhyracodon trigonodum*. It does not have the one really distinctive feature of the latter species, the confluent protoloph and metaloph on P 4/, forming a v with a median outlet for the valley, nor the somewhat loose attachment of the hypocone to the metaconule, notched by a deep valley posteriorly, on P 2/. In size, loss of C 1/, and general character, it resembles *Subhyracodon occidentale*.

The figures in Troxell's paper are accurate, except that they fail to show a small antero-internal descending rib, between the protoloph and ectoloph of P 1/ and the "mure" connecting the protocone and hypocone of P 2/.

***Subhyracodon gidleyi*, new species**

Figs. 29, 30, 31

The holotype, U. S. N. M. No. 11337, was collected by Mr. J. B. Hatcher in 1886, from the "White River Tertiary." It is slightly smaller than the type of *Subhyracodon occidentale*, from which the premolars are indistinguishable. The name is given for Dr. J. W. Gidley. M 1/ and M 2/ have part of the median valley completely cut off by the upgrowth of the antecrochet, to form medifossettes.

The specimen consists of left P 2/–M 2/, with the roots of P 1/ and fragments of M 3/, and right P 4/–M 2/, with the roots of P 1/–P 3/ and the front half of M 3/, fragmentary lower teeth, and the astragalus. Associated with it are *Mesohippus* and *Oreodon* teeth.

P 1/ had two roots. P 2–4/ have complete internal cingula. P 2/ has the protoloph and metaloph separate and parallel, but connected well above the level of the cingu-

lum. P 3/, rather worn, has the same character as the type of *S. occidentale*—or of most other members of the genus after a corresponding amount of wear. P 4/ has the character of *S. occidentale* or *S. copei*, in that the hypcone is a bud from the protocone, and the metaconule joins its anterior end. The molars have incomplete internal cingula. M 1/ is well worn. It has a medifossette completely cut off by the antecrochet. The internal cingulum, absent from the inner slopes of the two lophs, is very strongly developed across the valley, forming a dam of considerable height. M 2/ has no internal cingulum, except a slight one on the protocone, which does not close off the median valley. The antecrochet cuts off a deep medifossette. There is a faint trace of a crochet on the left side, but none on the right. The protocone of M 3/ interrupts the cingulum internally. There is a trace of the posterior buttress, and a distinct post-fossette. The molars have no external cingula, except a faint trace on the paracone of M 1/, and an extension along the ectoloph of M 3/ external to the posterior buttress.

The lower teeth are in very fragmentary condition, but they show unusually heavy cingula. Right P /2 is completely surrounded by a cingulum, except for a short space posteriorly. Left P /3 is almost completely surrounded by a cingulum, except for short interruptions by the metaconid and entoconid. The anterior, posterior, and external valleys are definitely enclosed at their feet. Right M /1 has a cingulum extending from the paraconid onto the metaconid, enclosing the anterior valley, and another from the metaconid to the entoconid, blocking the posterior valley.

The level of this form is not known. It gives a surprising mixture of characters, since the premolars are indistinguishable from *Subhyracodon occidentale*, and the molars, by themselves, would probably be referred to a new species of *Diceratherium* (in the restricted sense). It seems quite possible that the explanation of this apparent dis-

crepancy lies in the field of genetics, rather than of paleontology.

***Subhyracodon metalophum* (Troxell) 1921**

Aceratherium occidentale (Leidy). Osborn, 1898 (A. M. N. H. No. 1123, Pl. XIII, Fig. 1).

Cænopus tridactylus metalophus Troxell. Troxell, 1921 a (fig. 4).

"Holotype, No. 10245, Y. P. M. Probably Middle Oligocene, Rushville, Nebraska." Another specimen virtually identical with this, A. M. N. H. No. 1123, from the Upper Oreodon Beds, collected by American Museum Expedition of 1894, was described and figured by Osborn (1898). This form was larger than *Subhyracodon occidentale*, smaller than *Subhyracodon tridactylum* and probably hornless in both sexes. I 2/?, C 0/?, P 4/?, M 3/?. I 2/ is still large. The protoloph and metaloph of P 4/ are separate and parallel. The upper molars are smaller individually and collectively than in *Subhyracodon tridactylum* and have no secondary folds.

Osborn regarded this form as an advanced evolutionary stage of *Subhyracodon occidentale*, whereas Troxell considered it a primitive sub-species of *Subhyracodon tridactylum*. It is probably simplest to raise it to specific rank, and this would seem to be justified by its difference in character and level. Both stratigraphically and morphologically, it succeeds the typical *Subhyracodon occidentale*, and precedes the typical *Subhyracodon tridactylum*. Morphologically, it is also possible to derive it from *Subhyracodon trigonodum*. Stratigraphically, either form would answer equally well as an ancestor.

Y. P. M. No. 10254 has no trace of a mure on the upper premolars. In A. M. N. H. No. 1123, however, there is a mure on both P 4/'s, and on right P 2/ (omitted in Osborn's figure, 1898), but no trace of it on left P 2/.

The Effects of Wear in *Subhyracodon*

An old *Subhyracodon copei* would assume the same pat-

tern as an old *Subhyracodon occidentale*. A worn *Subhyracodon trigonodum* would be less easily distinguishable from a worn *Subhyracodon occidentale*. It would, however, never become absolutely identical with it, for P 4/ of the former would always have the protoloph and meta-loph forming a blunted v, whereas, in the latter, the metaconule would always hook on to the antero-external edge of the hypocone, so that the hypocone projects backward beyond the metaconule, although the extent to which it projects is progressively reduced by wear. A worn *Subhyracodon occidentale* may become indistinguishable from a worn *Subhyracodon metalophum*, and vice versa.

There is no reason to confuse the unworn pattern of any of the four species with any of the others.

Subhyracodon Brandt 1878

Anchisodon Cope 1879

The genoholotype is *Aceratherium quadriplicatum*.

Subhyracodon ? quadriplicatum (Cope) 1873

Hyracodon quadriplicatus (Cope) 1873

Aceratherium quadriplicatum (Cope). Cope, 1875.

Aceratherium (*Subhyracodon*) *quadriplicatum* (Cope). Brandt, 1878.

Anchisodon quadriplicatus (Cope). Cope, 1879.

Aceratherium quadriplicatum (Cope). Matthew, 1899.

Anchisodon quadriplicatus (Cope). Osborn and Matthew, 1909.

The holotype, A. M. N. H. No. 6339, from the (? Upper) Oreodon Beds, Cedar Creek, Logan County, Colorado, was collected by Professor Cope in 1873. It consists in the first and second left upper deciduous premolars and the first, second, and third right upper deciduous premolars. They are probably referable to some member of the genus *Subhyracodon*, even as here restricted, and, more likely than not, to *Subhyracodon occidentale* or *metalophum*, but they are not certainly determinable. The genus is regarded tentatively as a synonym of *Subhyracodon*, and the species as indeterminate.

Subhyracodon tridactylum (Osborn) 1893

Pl. XIII, fig. 8, and Pl. XVII, Osborn, 1898

Aceratherium tridactylum Osborn. Osborn, 1893.*Diceratherium proavitus* Hatcher. Hatcher, 1894.*Aceratherium tridactylum* Osborn. Osborn, 1898.*Cænopus tridactylus* (Osborn). Osborn and Matthew, 1909.*Cænopus tridactylus* (Osborn). Troxell, 1921 a.*Cænopus tridactylus proavitus* (Hatcher). Troxell, 1921a.*Diceratherium tridactylum* (Osborn). Osborn, 1923, b, p. 215.

The holotype is A. M. N. H. No. 538, a skull and nearly complete skeleton, collected by the Expedition of 1892, from the Protoceras Beds of South Dakota. Incipient horns are present in the males. I 2/2, C 0/0, P 4/(4)-3, M 3/3. I 2/ is small. The protoloph and metaloph of P 4/ are separate and parallel. Secondary wrinkles may appear on M 1/ or M 2/. I /2 is semi-erect to semi-procumbent. This species differs from *Subhyracodon metalophum* in its horizon, larger size, the presence of incipient horns on the male, greater length and width of the upper molars, occasional greater complication of the pattern of the upper molars, and the more frequent development of incipient mures on the upper premolars.

The type skull has an alveolus for the third left lower incisor and the first right lower premolar. The occasional presence of four lower premolars is almost certainly due to the abnormal retention of d P /1, a very small tooth, agreeing with what is unquestionably d P /1 in calves of *Subhyracodon occidentale* and *Subhyracodon tridactylum*. This tooth is both smaller and simpler than the P /1 (or possibly d P /1) of *Trigonias osborni* and *Trigonias ? gregoryi*. A calf lower jaw of *Subhyracodon tridactylum*, A. M. N. H. No. 1112, from the Protoceras Beds, has the formula I /2, C /0, d P /4 (M /1 just about to erupt). The alveolus for d P /1, which has dropped out, measures 12 x 8.5 mm.

Osborn's original description is incorrect in two points. The union of the post-glenoid and post-tympanic processes

in the type skull is apparently due to crushing. And, as Peterson pointed out (1911), the statement "no trace of fifth digit" is inexact, as the same nubbin representing metacarpal V, with its facet on the unciform, is present, as in *Subhyracodon occidentale* and *Menoceras cooki*.

If *Subhyracodon tridactylum* were transferred to the genus *Diceratherium*, as was done by Osborn (1923 b), it would have the advantage of making the latter genus nominally, as well as actually, monogenetic (see Miller, 1923, for definition of this term), according to the phyletic tree suggested below. However, it does not seem desirable to transfer a species to a different genus on quite such a slim basis, and this species really agrees more closely with *Subhyracodon occidentale*, the type of its genus, than with *Diceratherium armatum*, the type of the succeeding genus.

U. S. N. M. No. 11340 is apparently referable to this species, although it is very small, agreeing in size with the type of *S. occidentale*. Its red matrix suggests strongly that it came from the Oreodon Beds, but its level and exact locality were not recorded.

Diceratherium Marsh 1875

The genoholotype is *Diceratherium armatum* Marsh, Y. P. M. No. 10003, from the Lower John Day of Oregon. These were large Miocene rhinoceroses with paired horn cores on the nasals in the males, the females being hornless or nearly so. The horn cores are antero-posterior ridges, near to, but not on the ends of the nasals, and not knob-shaped. The upper cheek teeth are simple in pattern for Miocene rhinoceroses, with relatively few secondary crests and folds. A mure frequently occurs on the upper premolars.

The splitting off of *Menoceras* Troxell as a separate genus from *Diceratherium* Marsh is here tentatively accepted. The splitting off of *Metacænopus* Cook from *Diceratherium*, on the basis of sex characters, seems totally unwarranted, and *Metacænopus* (Cook, 1909) is here considered as congeneric with *Diceratherium*.

The following species seem to be quite certainly valid:
Diceratherium armatum Marsh — John Day and Great Plains

Diceratherium annectens (Marsh)—John Day

Diceratherium cuspidatum Troxell—John Day

Diceratherium lobatum Troxell—John Day

Diceratherium niobrarense Peterson—Great Plains

Diceratherium avum (Troxell)—Great Plains.

Y. P. M. No. 10235, "*Diceratherium* cf. *armatum*," from the Upper Oligocene, North Fork of the White River, collected by Mr. H. C. Clifford, resembles *Diceratherium armatum* so closely that there does not seem to be any reason against referring it definitely to that species. The only appreciable difference is the presence of a mure on P 4/, which is absent in the John Day form.

What seems the most plausible view of the interrelationships of the different species is given in the phyletic tree near the end of this paper.

***Diceratherium avum* (Troxell) 1921**

Cænopus tridactylus avus Troxell. Troxell, 1921 a (fig. 5).

The holotype is Y. P. M. No. 10251, collected by Mr. Brown from the Protoceras Beds of South Dakota. The animal was slightly larger than *Subhyracodon tridactylum*. There is a mure on P 2/ and P 3/. M 1/ and M 2/ have a crochet running from the metaloph which cuts off part of the median valley, giving an enclosed basin, as in *Subhyracodon gidleyi*, although smaller and arising in a different way.

This form was described and figured by Troxell, who regarded it as an advanced subspecies of *Subhyracodon tridactylum*. It seems sufficiently advanced over that form to deserve specific rank. Its greater size and the increasing complexity of the cheek teeth make it seem preferable to include it tentatively in *Diceratherium*. The intergradation of the two genera is so close, that any line of separation is rather arbitrary.

Diceratherium ? persistens (Osborn) 1904

Cænopus persistens Osborn. Osborn, 1904.

The type of this species is A. M. N. H. No. 9081, collected from the Miocene of Logan County, Colorado, by the Expedition of 1898.

This animal was probably a female dicerathere. The teeth are so worn that any specific determination would be highly questionable.

Paracænopus Breuning 1923

Genoholotype: *Præaceratherium filholi* (Osborn).

Aceratherium filholi Osborn. Osborn, 1900.

Præaceratherium filholi (Osborn). Abel, 1910.

Acerotherium filholi Osborn. Roman, 1912.

Paracænopus filholi (Osborn). Breuning, 1923.

The most useful figure of this species, in addition to Osborn's (1900), is published by Abel (1914). It shows the premolars in exactly the stage of evolution of *Subhyracodon occidentale*, with, however, a well-marked remnant of the posterior buttress on M 3/.

Breuning refers this genus to a new subfamily, the Cænopinæ. The closest resemblances of this genus would seem to be with *Subhyracodon* or with *Amphicænopus*, new genus, judging by the published figures. If it is eventually held to be congeneric with the former, it becomes, of course, a synonym. If it is congeneric with the latter, it takes precedence. That it is generically distinct from both is still another possibility.

Amphicænopus, new genus

The genoholotype is *Aceratherium platycephalum* Osborn and Wortman. This genus consists of very large, unprogressive Oligocene rhinoceroses, extending from the Titanotherium Beds to the Protoceras Beds. They are hornless in both sexes. The manus is unknown. P 3/ resembles *Trigonias gregoryi*, with the median valley escaping posteriorly. The internal cingulum on the premolars is complete, but, relatively, slightly weaker than in members of the genus *Subhyracodon*, as here restricted. The

internal cingulum on the upper molars is altogether absent, or very weak. When present, the chief trace surrounds the protocone of M 3/. A trace of the posterior extension of the ectoloph appears rather frequently on M 3/. I 2/ is procumbent. This genus shows its closest relationships to *Trigonias*, especially to *Trigonias paucidens*, and through it, to *Trigonias osborni* (see above). It seems probable that these two species are in its ancestral line. C 1/ is the first upper tooth to be lost, in this line.

This genus, as suggested by Osborn (1900), shows definite resemblances to *Paracænopus filholi* (Osborn). (See Abel 1910 and Roman 1912.) It is also remotely possible that it is related to the genus *Protaceratherium* Abel (1910). *Paracænopus* differs chiefly in having a well developed internal cingulum on the molars. Its premolar metamorphosis commences with P 2/, as in the American forms, but P 3/ is more advanced, whereas P 4/ is much more primitive, than in *Amphicænopus*. *Protaceratherium* resembles *Amphicænopus* in the reduction of the internal cingulum of the molars, but is much more advanced. Unless, however, the contrary is proved, it seems much more probable that the American forms are a separate line of autochthonous development, arising from *Trigonias*.

Amphicænopus platycephalus (Osborn and Wortman) 1894
Pl. XVIII, Osborn, 1893

Aceratherium platycephalum Osborn and Wortman. Osborn and Wortman, 1894.

Aceratherium platycephalum Osborn and Wortman. Osborn, 1893, Pl. XIII and XVIII.

Cænopus platycephalus (Osborn and Wortman). Osborn and Matthew, 1909.

Cænopus platycephalus (Osborn and Wortman). Troxell, 1921 a.

The holotype is a skull, A. M. N. H. No. 542. A. M. N. H. No. 540, consisting of right P 1/—M 3/ is the paratype. Both these specimens, and all other known specimens referred to this species, except A. M. N. H. Nos. 1478 and 12453, are from the Protoceras Beds. I 2—(1)/2, C 0/0,

P 4/4-3, M 3/3. I 1/2 is semiprocumbent. These are hornless rhinoceroses exceeding *Subhyracodon tridactylum* in size, with rather unprogressive premolars. The internal cingulum is complete and quite well developed on the upper premolars. P 1/ is relatively small, and simple in the slight development of its protoloph and metaloph. P 2/ is well advanced. Its protoloph and metaloph are parallel, and are separate until an advanced stage of wear. P 3/ is never molariform. Its hypocone is a conical cusp, distinct from both protocone and metaconule until a fairly advanced stage of wear, when it becomes confluent with the protocone. The principal outlet of the median valley is posterior. P 4/ is variable. In A. M. N. H. No. 540, it resembles P 3/ closely, with the hypocone an independent cusp, but more closely attached to the protocone, making the principal outlet of the median valley the posterior one. In the type, A. M. N. H. No. 542, the deepest outlet of the median valley is internal, on both sides. Right P 4/ has the hypocone attached to the metaconule, though it may well have been separate in the unworn tooth. Left P 4/ is more molariform, and resembles some specimens of *Subhyracodon tridactylum*. There is no internal cingulum, except a rudiment in the valley on M 1/ and M 2/. M 3/ apparently has none in the type, but a nearly complete, although rather faint one in the paratype.

In the original description (Osborn & Wortman, 1894), the type is given as No. 545. Osborn (1898, page 140) gives No. 542 as the type. No. 540 is given as co-type (= paratype) in 1894, and in 1898 on page 140. In the same paper, however (Osborn 1898, page 141 and Plates XIII and XVIII), No. 540 is referred to as the type, and No. 542 as the co-type. This confusion can be cleared up definitely, as the type description is of the skull, No. 542, although, by a misprint, it is called No. 545. The set of right cheek teeth, No. 540, is therefore the paratype.

Osborn (1898) described the lower jaw from A. M. N. H. No. 1444. Its most diagnostic character is the large

size of the teeth and the jaw.

***Amphicænopus platycephalus* ? (Osborn and Wortman)**

Aceratherium platycephalum Osborn and Wortman. Osborn, 1898, p. 141, A. M. N. H. No. 1478.

This description is based on A. M. N. H. No. 1478, collected by Mr. J. W. Gidley, in 1896, from the Titanotherium Beds, Sand Creek, Hat Creek Basin, Nebraska. I 1/(3)-2, C 0/0, P 4-3/4-3, M 3/3. The specimen consists of the skull with the lower jaw, with P 2/-M 3/ of both sides, left P /4-M /3 and right M /2 and M /3, with cervicals 2-5, and a metatarsal, and both I 1/'s, right I /1-2, left I /1-3, left P /1-3 and right P /2-M /1, represented by their alveoli. The individual was very old, and the teeth are exceedingly worn, so that most of the pattern is obliterated. The following characters are still apparent. The internal cingula on the upper premolars are complete, but not especially prominent. P 4/ has the hypocone still connected with the protocone (although partly separated from it by a groove, internally), allowing the median valley to escape posteriorly. Both third upper molars retain faint traces of the posterior buttress. The upper molars are without an internal cingulum. There are very small alveoli for the third left lower incisor and the first left lower premolar, but there is no trace of either on the right side.

It is rather probable that a younger specimen would show differences of specific value from *Amphicænopus platycephalus*, but it seems best to allow the new species, if it is one, to be founded on some less nondescript type specimen. A younger specimen would be likely to show a closer approach toward *Trigonias paucidens*. If a new species were named from this specimen, the chief character would have to be its horizon. There are minor morphological differences. It is slightly smaller throughout. The mandible is much shallower under P /2. The lower jaw of *Amphicænopus platycephalus*, A. M. N. H. No. 1444, has a double mental foramen under the lower incisor tusk. In

this specimen it is single, under P /1 on the left and anterior to P /2 on the right side. The character of this foramen, however, seems to be very variable and of little or no diagnostic importance. Judging from the characters that are still preserved, this form is noticeably more advanced than *Trigonias paucidens*, in the loss of I 3/ (and I 2/??), in the increase in size of the hypocone of P 4/ and in its closer approach to separation from the protocone.

A. M. N. H. No. 12453, collected by Mr. H. F. Wells in 1905, from the Upper Titanotherium Beds, Cane Creek, South Dakota, a very badly damaged lower jaw, has the same abnormally slender rami as No. 1478. This may turn out to be a good specific character.

Amphicænopus ? simplicidens (Cope) 1891 Fig. 43, Osborn, 1898
Cænopus simplicidens Cope. Cope, 1891.

Aceratherium simplicidens (Cope). Osborn and Wortman, 1894.

Cænopus (= *Subhyracodon*) *simplicidens* (Cope). Osborn and Matthew, 1909.

Cænopus simplicidens Cope (of doubtful validity). Troxell, 1921 a.

The holotype is A. M. N. H. No. 10708, from the Oligocene, Big Badlands, S. D., consisting of the third left upper molar with rather more than half of the second left upper molar attached to it. It is not determinable specifically, nor, with absolute certainty, generically. M 2/ has no internal cingulum, M 3/ has a weak one. It is more probably *Amphicænopus* cf. *platycephalus* than anything else, but might almost equally well be referred to as *Trigonias* cf. *osborni* or to *Trigonias* cf. *paucidens*, and other references might be conceivable. The degree of resemblance certainly does not warrant reducing *Amphicænopus platycephalus* to synonymy. This "species" has only an antiquarian interest and should be dropped from faunal lists.

DISCUSSION

There are several interesting conclusions that can be drawn from the last table. It would appear that the ratios Mtc III/R, and, to a lesser extent, Mts III/T, tend to be

Table V a

<u>Geonopus</u> <u>mitis</u> Paratype A.M.N.H. 6325	<u>Subhyracodon</u> <u>copel</u> Holotype A.M.N.H. 522	<u>Subhyracodon</u> <u>copel</u> A.M.N.H. 5326	<u>Subhyracodon</u> <u>trigonodum</u> Holotype A.M.N.H. 528 Paratype 529	<u>Subhyracodon</u> <u>"trigonodum</u> <u>allum</u> " Holotype Y.P.M. 12052	<u>Subhyracodon</u> <u>occidentale</u> Neotype U.S.N.M. 114	<u>Subhyracodon</u> <u>occidentale</u> A.M.N.H. 6330	<u>Subhyracodon</u> <u>gidleyi</u> Holotype U.S.N.M. 11337	<u>Subhyracodon</u> <u>metaloshum</u> Holotype Y.P.M. 10254							
R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L
I ¹ - C ¹ over all	---	48	48	---	---	---	---	---	---	---	---	---	---	---	---
A-P diam. I ¹	---	20.5	18	---	---	23.5	24	---	---	---	---	26	24	---	---
Tr. diam. I ¹	---	9.5	10.5	---	12.5	10	11	---	---	---	---	11	11	---	---
Crown-length of I ¹	---	---	---	---	---	No. 528 7.5	12	13	---	---	---	---	---	---	---
A-P diam. I ²	---	13.5	13.5	---	17	9	10	13	---	---	---	---	---	---	---
Tr. diam. I ²	---	9.5	9.5	---	12.5	5.5	7.5	8	---	---	---	---	---	---	8.5
Crown-length of C ¹	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
A-P diam. C ¹	---	7.5	5	---	4.5	---	---	---	---	---	---	---	---	---	---
Tr. diam. C ¹	---	6	7	---	7	---	---	---	---	---	---	---	---	---	---
Diastema	---	36	38	---	34	---	37	37	---	37 +	---	---	---	---	36
Length, P ¹ -M ³	---	158.5	158.5	---	---	174	---	---	---	182	---	---	---	---	196
Length, P ² -M ³	---	145	144	---	---	160.5	163.5	---	---	165	---	---	163	---	176.5
Length, P ¹ -4	69.5	---	76.5	76.5	---	---	82.5	---	96	94	85	85	---	---	95
Length, P ² -4	58	---	59.5	80	59	---	68.5	69.5	76	73.5	72	67	---	62.6	76
Length, M ¹ -3	---	84.5	83	---	---	100.5	101.5	---	---	---	100	108.0	---	108	103
Length, P ¹	13	---	17	17.5	---	---	17.5	---	20	20	---	19	---	---	20
Width, P ¹	---	16.5	16	---	---	18	---	17.5	18	---	---	---	---	---	19.5
Length, P ²	17	---	18.5	20	18	---	20	19.5	23.5	22.5	22.3	20.6	---	19.4	25
Width, P ²	23	---	24.6	25	23	---	---	22.5	26	26	---	26	---	25.0	30
Length, P ³	19	---	20.5	20.5	19	---	23	22	26	26	21.5	22.3	---	21.0	26
Width, P ³	28	---	29.5	29	27.5	---	31	31	33.5	33	---	34.1	---	27.3	36
Length, P ⁴	20	20	20.5	21.5	---	---	22.5	23	26	26.5	24.3	23.5	27.0	22	22.6
Width, P ⁴	33.5	33.5	32	32	---	---	33.5	32	37	37	---	37	36.5	31.8	32
Length, M ¹	27	27	26	26.5	27	29	28.5	33	33	31	30.5	33.0	29	28.3	34
Width, M ¹	33	33	32.5	33	31	31.5	36	36.5	37	37.5	---	38.8	---	34.0	39.5
Length, M ²	---	30.5	29	28.5	29.5	---	34	34	37	38	36	34.6	35.7	31	32
Width, M ²	---	36	35.5	36	35	---	38.5	38.5	39.5	40	---	41.5	42.0	36.5	36
Length, M ³	---	---	29.5	29.5	33	---	31.5	32	---	---	---	34.5	36.0	---	36
Width, M ³	---	---	33.5	34	---	---	38.5	39	---	---	---	40.5	39.0	---	37
No. 529															
Tip nasals to oc. crest	---	---	406.5	402	---	---	431	434.5	---	---	---	---	---	---	---
Max to oc. condyle	---	---	409.5	406.5	---	---	---	---	---	---	---	---	---	---	461
Greatest width across zygomas	---	---	198	---	---	---	198.5	---	---	---	---	---	---	---	---
Depth incision ant. nares	---	---	77.5	73	---	---	80.5	85.5	87	87	---	---	---	---	---
Height occiput above condyle	---	---	116	111.5	---	---	115.5	112	---	---	---	---	---	150	157
Least width bet. M and L. P ³ 's	---	---	30.6	---	---	---	41	---	---	---	24.6	---	---	---	---
Least width bet. R and L. M ³ 's	---	---	52.5	---	---	---	59	---	---	---	48.4	---	---	---	---

Table V b

	Subhyracodon metalophum		Subhyracodon tridactylum		Subhyracodon proavitus		Diceratherium avus		Diceratherium lobatum		Amphicaenopus platycephalus		Amphicaenopus platycephalus		Amphicaenopus platycephalus ?		Amphicaenopus ? simplicidens	
	A.M.N.H. 1123		A.M.N.H. 538		P.U. 10965		Y.P.M. 10261		Y.P.M. 12487		Holotype 542		Paratype A.M.N.H. 540		A.M.N.H. 1478		Holotype A.M.N.H. 10708	
	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	L	
I ¹ - C ¹ , over all	----	----	56.5	----	----	----	----	----	----	----	----	----	----	----	----	----	----	
A-P diam. I ¹	✓ 22	----	28	29	----	----	----	----	20.5	20	----	----	----	----	21.5	21.5	----	
Tr. diam. I ¹	✓ 11.5	----	13.5	12	----	----	----	----	8.5	8.5	----	----	----	----	9	9	----	
Crown-length I ²	----	----	12	13	----	----	----	----	9.5	11	----	----	----	----	----	----	----	
A-P diam. I ²	✓ 18.5	----	9.5	9.5	----	----	----	----	13	14	----	----	----	----	----	----	----	
Tr. diam. I ²	✓ 9.0	----	8	6.5	----	----	----	----	7	7	----	----	----	----	----	----	----	
Crown-length C ¹	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	
A-P diam. C ¹	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	
Tr. diam. C ¹	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	
Dinastema	44.0	----	51.5	60	----	----	----	----	57	51	----	----	----	----	107	----	----	
Length, P ¹ -M ³	----	196.5	215	221	----	----	----	----	----	----	236	238	241	234	----	----	----	
Length, P ² -M ³	176	176	↑ 198	----	----	----	----	----	----	----	217	226	220.5	216.5	216	----	----	
Length, P ¹ -4	----	94	↑ 102.5	↑ 107.5	97	96.7	109	111	116	116	94	99.5	116	116.5	----	----	----	
Length, P ² -4	74.5	73.5	↑ 83.5	↑ 86	76.6	75.6	86	90	83	83	79	86	84.5	87.5	86	----	----	
Length, M ¹ -5	106.0	106	↑ 118	----	----	----	----	----	----	----	138.5	141	136	129	131.5	----	----	
Length, P ¹	----	21.5	22	23	21.0	21.0	23	25	----	25	----	----	23.5	----	----	----	----	
Width, P ¹	----	21.0	21	21	20.8	22.4	23.5	21	----	21	----	----	17	----	----	----	----	
Length, P ²	22.0	22.0	↑ 24	↑ 26	24.5	24.6	26.5	26	25	26	----	23.5	23.5	26	26	----	----	
Width, P ²	28.5	30.0	↑ 34	----	31.5	32	33	31	33	33	----	36.5	29	33	34	----	----	
Length, P ³	26.0	25.0	↑ 29	↑ 29	24.4	25.4	28	30	33	33.5	27.5	27.5	27	30	29	----	----	
Width, P ³	37.5	37.0	----	----	37.3	39.0	39.5	39	46	46	----	41.5	40.5	42.5	41	----	----	
Length, P ⁴	25.5	25.5	↑ 31	↑ 31	27.0	27.0	↑ 33.5	↑ 34	34	33.5	33	33	33	31	30	----	----	
Width, P ⁴	40.0	40.5	----	----	43.4	43	↑ 37	----	50	50	49	48	48.5	48	47.5	----	----	
Length, M ¹	32.5	34	↑ 37	↑ 36	35.4	32.7	38	37	----	45.5	45	44.5	41	37.5	38	----	----	
Width, M ¹	40.0	39.0	----	----	----	44.5	44	43	----	54	54.5	53	53	51.5	----	----	----	
Length, M ²	36.0	36.0	↑ 45	----	38.2	37.5	----	40	----	----	45	47.5	48.0	46	46	----	----	
Width, M ²	44.0	44.0	----	----	----	47	46	43	----	53	56	58	58.5	58.5	57	↑ 50	----	
Length, M ³	35.0	35.0	41.5	----	----	----	----	----	----	----	48	50	48	47.5	48	42.5	----	
Width, M ³	40.0	40.0	----	----	----	----	----	----	----	----	57	56.5	53	57.5	57	47.0	----	
Tip nasale to oc. crest	----	----	↑ 510	----	496	492	----	----	----	----	62.5	----	----	----	----	----	----	
Pmx. to oc. condyle	468	----	↑ 502	----	----	----	----	----	----	----	----	----	----	----	----	----	----	
Greatest width across zygomas	----	----	----	----	281	----	----	----	----	----	↑ 360	----	----	293	----	----	----	
Depth incision ant. nares	----	----	106	108	106	108	----	----	----	----	125	118.5	----	----	----	----	----	
Height occiput above condyle	----	----	176	----	----	153	----	----	----	----	141.5+	----	158+	162.5+	----	----	----	
Least width bet. R. and L. P ² 's	----	----	----	----	----	----	----	----	----	----	56	----	----	----	----	----	----	
Least width bet. R. and L. M ³ 's	----	63.0	----	----	----	----	----	----	----	----	83	----	68	----	----	----	----	

d, deciduous

e, estimated

t, measured along
ectoloph

v, alveoli only

d, deciduous

e, estimated

t, measured along
ectotoph

v, alveoli only

Table VI

	<u>Caenopus</u> <u>mitis</u> Holotype A.M.N.H. 6525		<u>Caenopus</u> <u>dakotensis</u> Holotype A.M.N.H. 1110		<u>Subhyracodon</u> <u>trigonodum</u> Holotype A.M.N.H. 529		<u>Subhyracodon</u> <u>trigonodum</u> <u>allum</u> Holotype Y.P.M. 12062		<u>Subhyracodon</u> <u>tripactylum</u> Holotype A.M.N.H. 538		<u>Amphicaenopus</u> <u>platycephalus</u> A.M.N.H. 1444		<u>Amphicaenopus</u> <u>platycephalus</u> ? A.M.N.H. 1478		<u>Amphicaenopus</u> <u>platycephalus</u> ? A.M.N.H. 12453	
	R	L	R	L	M	L	R	L	R	L	R	L	R	L	R	L
Tip I ₁ to back of I ₃	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Crown length of I ₁	---	---	---	---	---	---	---	---	9.0	---	---	---	---	---	---	---
A-P diam. I ₁ at root	---	---	---	---	---	---	---	---	7.5	---	6	6	6	6	---	---
Tr. diam. I ₁ at root	---	---	---	---	6	5.5	---	---	7.0	---	6	6	6	4.5	---	---
A-P diam. I ₂	9	9	9	---	---	14.5	---	---	22.0	19.0	---	32.5	24.5	27.5	---	---
Tr. diam. I ₂	---	10 +	13	---	---	21	---	---	28.0	30.0	---	38.5	19.5	15.5	---	---
Crown length I ₃ from root	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
A-P diam. I ₃ at root	---	---	---	---	---	---	---	---	---	---	---	---	---	6	---	---
Tr. diam. I ₃ at root	---	---	---	---	---	---	---	---	---	---	---	---	---	6	---	---
Diastema	---	---	22	---	3	18	---	---	55.0	66.5	---	73	78	58.5	---	---
P ₁ - M ₃	---	---	---	---	---	---	---	---	---	---	---	---	---	22.0	---	---
P ₂ - M ₃	---	---	124	127.5	170	---	---	---	205.5	206.5	---	221	213.5	212.5	226	224
P ₁₋₄	---	---	---	---	---	---	---	---	---	---	---	---	---	91	---	---
P ₂₋₄	---	57	48.5	50	66	---	---	---	85.0	89.0	---	82	90	82.5	---	---
M ₁₋₃	87	---	75.5	77	105.5	---	---	---	122.0	---	---	142	132.5	132	---	140
P ₁ , length	---	---	absent	---	absent	---	---	---	---	---	---	---	---	---	---	---
P ₁ , width	---	---	absent	---	absent	---	---	---	---	---	---	---	---	---	---	---
P ₂ , length	---	14.5	13.5	---	21.5	---	---	---	26.0	25.0	---	19.5	---	---	---	---
P ₂ , width	---	8	---	---	12.5	---	---	---	16.5	---	---	14.5	---	---	---	---
P ₃ , length	---	19.5	17.0	---	25.5	---	---	---	31	---	---	31	---	---	---	---
P ₃ , width	---	11	13.5	---	16	---	---	---	---	---	---	24.5	---	---	---	---
P ₄ , length	---	18	18.5	18.0	24	---	---	28	31	---	---	32	---	32.5	---	---
P ₄ , width	---	12	14.5	14.5	18	---	---	20.5	---	---	---	30.5	---	27	---	---
M ₁ , length	25	26	20.0	21.5	28.5	---	33.5	33.5	85	---	---	40.5	---	40	---	---
M ₁ , width	e 19	17.5	15.5	---	27	---	21	21	---	---	---	33	---	32.5	---	---
M ₂ , length	e 28	---	27.5	27.0	37	---	38	36.5	42	---	---	50	46.5	46	---	---
M ₂ , width	e 19	---	16.5	16.5	23	---	20.5	22.5	---	---	---	36	33	34	---	---
M ₃ , length	31	---	27	27	40.5	---	---	---	44	---	---	55.5	51.5	54.6	---	55.5
M ₃ , width	e 19	---	16	15.5	22	---	---	---	---	---	---	33.5	32	33	---	33.5
Symphysis to angle	---	---	252.5	271.5	331	---	---	---	45?	---	529	513	507	---	---	---
Coronoid above angle	---	---	146 +	140.5 +	180	---	---	170 +	e 261	---	---	252.5	249	---	---	---
Length of symphysis	45	---	48.5	---	61	---	---	---	103	---	126	98.5	---	100	---	---
Depth ramus below P ₂	---	40	38.5	---	45	---	---	---	70	---	---	84	57	60	---	53
Depth ramus below M ₂	---	---	48.5	45.5	52	---	53.5	54	e 74.0	---	e 93	84	86	83	---	55

TABLE VII

	Humer- us (H)	Rad- i- us (R)	Met- a- car- pal III (Mts.) III	R/H (H=1) H R=1	Fe- mur- ia (F) (T)	Met- a- tar- sal III (Mts.) III	T/F (F=1)	MtsIII F T = 1	MtsIII T T = 1			
<i>Opsic. (Ceratotherium) sinu-</i> A.M.N.H. #5185E	495	417	187	.85	.38	.45	523	397	175	.76	.34	.44
<i>Opsiceras bicornis</i> A.M.N.H. #27757	475	414	190	.87	.40	.46	495	376	172	.76	.35	.46
<i>Didermoceros sumatransis</i> A.M.N.H. #54763	412	313	159	.76	.39	.51	446	326	145	.73	.33	.44
<i>Subhyracodon tridactylum</i> A.M.N.H. #538	363	289	145	.79	.40	.50	423	303	130	.83	.31	.37
<i>Caenopus mitis</i> , perhaps mixed with <i>S. coqui</i> , A.M.N.H. #6325		204					291	234		.80		
<i>Trigonias osborni</i> C.M. # 95	306	262	126.5	.86	.41	.48						
<i>Teleoceras fossilizer</i> ^x	305 ^e	238	114	.78	.37	.48	408	233	105	.57	.26	.45
<i>Metamynodon planifrons</i> ^x	393	320	152	.81	.39	.48	480	280	118	.58	.25	.42
(After Peterson) <i>Menoceras coqui</i>	250	250	138	1.00	.55	.55	323	275	125	.85	.39	.45
<i>Hyracodon apertum</i> P.H. # 11414	227	218	123	.96	.54	.56	260	230	118	.86	.45	.51
<i>Prothyraodon obliquidens?</i> C.M. # 2942	140	146	72.5	1.04	.52	.49						
<i>Triplopus cubitalis</i> A.M.N.H. # 5095	112	145	70	1.29	.62	.48						
<i>Hyrcodus exilis</i> ^x	197	197	93	1.00	.47	.47	254	243	110	.96	.43	.45
<i>Hyrcodus affinis gracilis</i> X.P.H. #11173		154	79		.51	.54	154		83		.54	
<i>Hyrcodus</i> , from Huairao A.M.N.H. #17435	198.	175.	93.	.88	.47	.53	251	235		.84		
<i>Echippus</i> sp. ^x	121	110	64	.91	.53	.58	162	162	85	1.00	.51	.51
<i>Euprotogonia puercoensis</i> ^x							105	107	45	1.02	.43	.42

x, After Gregory
e, estimated

quite stable in the Rhinocerotidae. The great divergence of *Triplopus* in R/H from all other rhinoceroses, even the most highly cursorial, is an evidence of its remarkably high cursorial specialization, which seems even more out of place on account of its very early age. The two living African rhinoceroses are seen to be very close together, throughout. This is probably due to the combination of rather close relationship and generally similar habitus. The striking parallelism between *Teleoceras* and *Metamynodon*, and between *Menoceras*, *Hyracodon*, and *Hyrachyus*, may be regarded as due solely to convergence in members of the same general group. The first case represents a semi-aquatic, hippopotamus-like development; whereas the second represents a fairly high degree of cursorial adaptation. Various other deductions of a less striking character could be drawn.

The new genus, *Eotrigonias*, throws the first definite light on the Eocene history of the true rhinoceroses. Study of the genus *Trigonias* shows the close resemblance of *Trigonias osborni* to *Eotrigonias rhinocerinus* leading, in the other direction, through *Trigonias paucidens* to the *Amphicænopus* line. The trace of a posterior buttress on

M3/ in most specimens of *Trigonias osborni*, as well as its sporadic occurrence in other Oligocene forms, is of considerable interest as showing a retention of, or reversion toward, the primitive condition.

The generic names, *Trigonias*, *Cænopus* and *Diceratherium* as generally used in the past, represent a horizontal classification and not a vertical, or truly genetic one. *Trigonias* is "multiserial," and *Cænopus* and probably, *Diceratherium* are "polygenetic"; but the American Eocene and Oligocene Rhinocerotidae as a whole are only multiserial. There is no evidence whatever that they are polygenetic (See Miller, 1923, for definitions of these terms). For this reason, the "*Cænopus*" group is split into three genera, and the splitting off of *Menoceras* from *Diceratherium* is tentatively accepted.

Osborn's division (1898) of the American Oligocene Rhinocerotidæ into two series, largely on the basis of the position of the premolar hypocone, is in part artificial, since this character is chiefly indicative of the stage of evolution. His series "II" is, in all probability, a real one, but his series "I" is composite and artificial. Series "II," the *Subhyracodon copei-Diceratherium armatum* line, has gradually been confirmed in increasing detail.

Osborn's statement (1898) of the methods of metamorphosis of the upper premolars in the Oligocene rhinoceroses can now be restated more clearly and accurately, and in greater detail. (It will be noted that the method differs in almost every respect from that followed by the horses.) The metamorphosis of the upper premolars in the true rhinoceroses, hyracodonts and hyrachyids takes place as follows:

1. The protoloph, consisting of the protocone and protoconule, is the main transverse crest, the metaconule being a minor crest abutting on the protocone. *Hyrachyus*, *Prothyracodon*.

2. The protocone elongates antero-posteriorly, and the hypocone commences to split off from it. *Eotrigonias*, *Hyracodon petersoni*, *Trigonias osborni*. In both these stages, the median valley opens posteriorly.

3 a. The hypocone is, for a time, a separate cusp, conical in *Trigonias gregoryi*, *Amphicænopus platycephalus*, and elongate in *Metahyrachyus bicornutus*.

3 b. The hypocone unites with the metaconule before separating from the protocone, giving an enclosed basin. *Tripopus* ? (cf. *Lophialetes*), *Hyracodon arcidens*, *Leptacceratherium trigonodum*, *Subhyracodon occidentale*, *Colonoceras agrestis*.

(*Cænopus mitis* is already so progressive, that the question which course its ancestors took must be left open, but,

judging from P 3/, it followed 3 b. Osborn's putting this species in "I" is apparently based on the assignment of a specimen of *S. copei* to this species as paratype.

3 x. P 2/ is most progressive, *Trigonias*, *Amphicænopus*, *Subhyracodon*, *Hyrcodon petersoni*.

3 y. P 4/ is most progressive. *Hyrachyidæ*, *Amynodontidæ*, *Cænopus mitis*, most European true rhinoceroses, *Hyrcodon nebraskensis*, *H. apertus*.

4. P 2/—P 4/ have all become molariform, with the protoloph and metaloph separate and parallel. *H. leidyani* and the Miocene to recent rhinoceroses.

There does not seem to be any reason to attach profound significance to these differences in the exact order of appearance of equivalent stages in different lines. The hereditary material of these forms must have been fundamentally similar; it is entirely to be expected that the same characters should appear in the various lines, but in different order.

The method of metamorphosis of the upper molars in the *Amynodontidæ* is uncertain, as they are already well advanced when they first appear. It seems rather likely that the metaloph is developed from the metaconule only, and that no hypocone ever developed, giving still another mode.

Metamorphosis of the lower premolars takes place as follows in the *Hyrachyidæ*, *Triplopodinæ*, and *Hyrcodontinæ*:

1. The hypoconid is a simple antero-posterior ridge, well below the level of the trigonid.

2. The entoconid appears as a separate, low, conical cusp.

3. The entoconid elongates transversely, reaching the base of the hypoconid, but not attaining its height.

4. The hypoconid and entoconid fuse into a continuous, asymmetrical crescent, as in the molars.

Judging from the condition in some specimens of *Trigonias osborni*, the earliest true rhinoceros in which the lower premolars are known, the Rhinocerotidæ follow a similar course, except that instead of stage 3, the hypoconid throws off a hook mediad which fuses with the conical entoconid. The method followed by the Amynodontidæ is unknown.

Peterson (1920) and Troxell (1922 a) have endorsed Marsh's suggestion (1877) that the horned rhinoceroses of the Miocene were descended from the horned Eocene forms (*Colonoceras* and *Metahyrachyus*). This seems highly improbable. The horns are rather too far posterior on the nasals to give rise to the condition in *Menoceras*. But a more important objection is the great improbability that the true rhinoceroses are polygenetic, still more that any true rhinoceros could be derived from a Bridger hyrachyid, especially in view of the degree of advancement of the genus *Eotrigonias*. The ancestry of *Diceratherium* (as restricted by Troxell) seems too definitely established to make it necessary to consider this suggestion as applied to it. *Metahyrachyus bicornutus* seems clearly worthy of generic distinction, and shows, as Troxell has pointed out, a number of resemblances to true rhinoceroses. The horn cores are so far posterior, however, that it seems highly unlikely that it could have been ancestral to any other known rhinoceros. Comparison with *Eotrigonias* indicates that it is simply the most progressive of the hyrachyids, paralleling the true rhinoceroses in some respects.

The terms "Diceratheriinae" and "Aceratheriinae," when used in their customary complimentary sense for the horned and hornless American forms, are useless and misleading, and should be abandoned. If they are to be replaced at all, which seems of doubtful utility in the present state of our knowledge, they should be replaced by names indicating the separate lines of development.

Phyletic trees are extremely useful, if regarded as tentative summaries of contemporary knowledge. It is

much easier to deal intelligently with a group of related forms if they can be visualized as a unified whole, in their probable or possible relations to each other, rather than as a series of isolated items in a card catalogue. And certainly, in principle at least, the phylogenetic viewpoint is closer to the truth. The "family tree" (fig. 1) is given as my interpretation of the most probable relationships of the forms discussed in this paper and of a few others. The assumed lines of descent are based primarily on tooth structure, secondarily on the structure of the limbs. The subdivision of the old "*Cænopus*" agglomeration also coincides with the bodily size of the different groups, giving series of small, intermediate, and very large forms.

In regard to relative level of different forms in the Titanotherium Beds, Dr. Matthew states (verbal communication) that it does not seem possible to correlate, even between finds in different parts of the same general area. He believes that these deposits were made by streams which were constantly shifting their beds, and that the top of the beds in one locality may be equivalent to their bottom a few miles away. However, in the chart, forms from the Titanotherium Beds are placed in the level given by the collector, whenever it was recorded.

SUMMARY

1. During the lower Eocene, the rhinoceroses apparently split into four main lines, the little-modified descendants of the primitive type, the Hyrachyidæ; the Amynodontidæ; the Hyracodontidæ, which shortly split into two divergent lines, the Hyracodontinæ and the Triplopodinæ; and the Rhinocerotidæ.

2. The Hyrachyidæ kept most of their primitive heritage. The manus was always tetradactyl. No teeth were lost, except P /1. The premolars never became molari-form. The cusps of the upper molars never fully lost their separate identity by fusion into lophs.

3. The Amynodontidæ increased progressively in bulk. The tetradactyl manus was retained, and horns were never developed. The canines and molars increased enormously in size, whereas the incisors and premolars were reduced in number and size.

4. The Hyracodontidæ developed cursorially, with tri-dactyl manus. The Hyracodontinæ achieved moderate cursorial specialization and the premolars became progressively molariform. The Triplopodinæ developed aberrantly, achieving great cursorial specialization associated with primitive or aberrant premolar characters.

5. The Rhinocerotidæ, appearing in the Middle Eocene of America, developed, first as tetradactyl, then as tridactyl forms, with I 1/ and I 2/ greatly enlarged, and with progressive reduction of the other front teeth. The posterior buttress of M 3/ was soon lost. In the Oligocene of North America, there were three main lines of evolution, the small forms such as *Cænopus mitis* with P 2/ and P 4/ molariform; the larger forms such as *Subhyracodon occidentale*, in which metamorphosis commenced with P 2/, and the still larger series including *Trigonias* and *Amphicænopus platycephalus*, in which the premolar metamorphosis was much retarded.

6. Premolar metamorphosis in the rhinoceroses seems to occur as follows. In the upper teeth, the protocone elongates antero-posteriorly, and develops an incipient separation across the middle, marking off the posterior half as the hypocone. Either at this stage, or else after the separation is complete, the metaconule becomes attached to the hypocone, forming a complete metaloph. As a result, the median valley opens internally instead of posteriorly. There is a gradual backward rotation of the metaloph, until it becomes approximately parallel with the protoloph. This is accomplished partly by backward migration of the hypocone, partly by shifting the outer attachment of the metaconule anteriorly.

Metamorphosis of the lower premolars takes place as follows in the Hyrachyidæ, Triplopodinæ, and Hyracodontinæ:

1. The hypoconid is a single, antero-posterior ridge, well below the level of the trigonid.

2. The entoconid appears as a separate, low, conical cusp.

3. The entoconid elongates transversely, reaching the base of the hypoconid, but not attaining its height.

4. The hypoconid and entoconid fuse into a continuous, asymmetrical crescent, as in the molars.

Judging from the meagre evidence, the Rhinocerotidæ follow a generally similar course, except that instead of stage 3, the hypoconid sends of a hook mediad, which fuses with the conical entoconid. The method followed by the Amynodontidæ is unknown.

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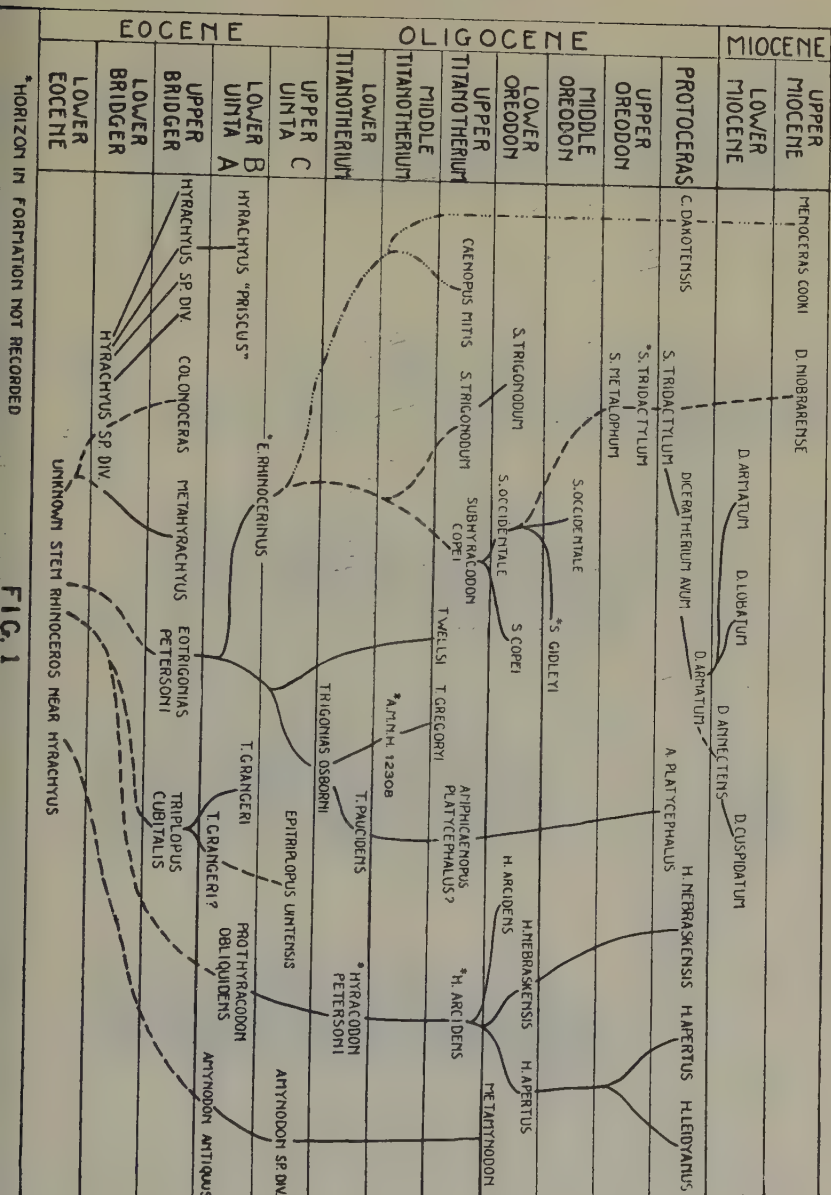
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EXPLANATION OF FIGURES

EXPLANATION OF
PLATE 1

Fig. 1. Phylogenetic Chart.

Page 81.



EXPLANATION OF

PLATE 2

FIGURE

2. *Triplopus cubitalis*, type, A. M. N. H. No. 5095, right manus, x 1.

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3. *Triplopus cubitalis*, type, A. M. N. H. No. 5095,
L P 1/-M 3/ (M 2-3/ reversed from right side), x 1.

4. *Triplopus cubitalis* ? A. M. N. H. No. 2344,
R C /1-M /3, x 1.

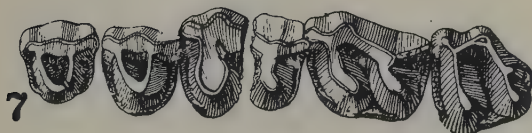
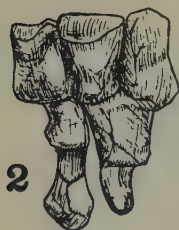
5. *Triplopus grangeri*, type, A. M. N. H. No. 1972,
R M /1-3, x 1.

6. *Triplopus grangeri*, type, A. M. N. H. No. 1972,
L P 4/-M 3/, x 1.

7. *Triplopus grangeri* ?, C. M. No. 2336, L P 3/-M 3/, x 1.
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8. *Hyracodon nebraskensis*, A. M. N. H. No. 12460
L I /1-C /1, x 1.

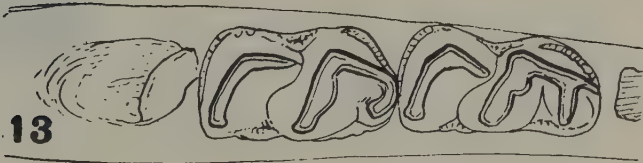
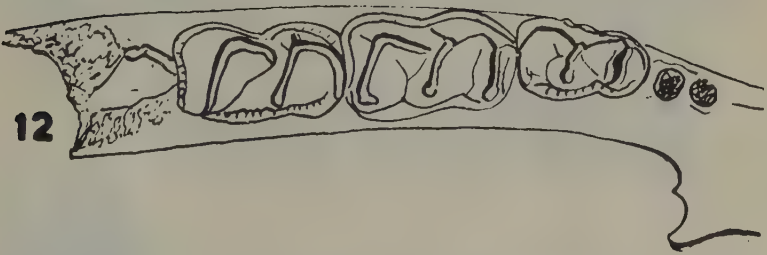
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EXPLANATION OF
PLATE 3

FIGURE

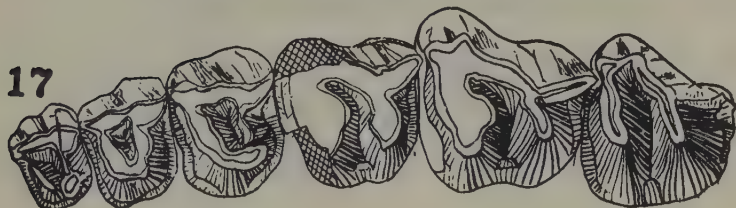
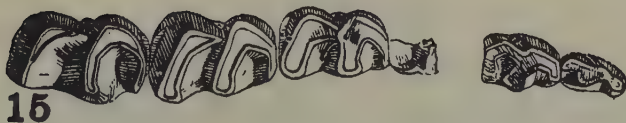
9. *Epitriplopus uintensis*, type, C. M. No. 3007 a,
L P 1-3/, -d P 4/, M 1-3/, x 1.
Page 19
10. *Prothyracodon obliquidens*, A. M. N. H. No. 1971,
R P 2/ - M 3/, x 1.
11. *Prothyracodon obliquidens*, A. M. N. H. No. 1971.
L P /1 - M /3, x 1.
Page 22
12. Young *Hyracodon* sp., C. M. No. 318,
L d P /3 - M /1, x 1.
13. Young *Hyracodon* sp., C. M. No. 3581,
L d P /4 - M /1, x 1.
Page 28



EXPLANATION OF
PLATE 4

FIGURE

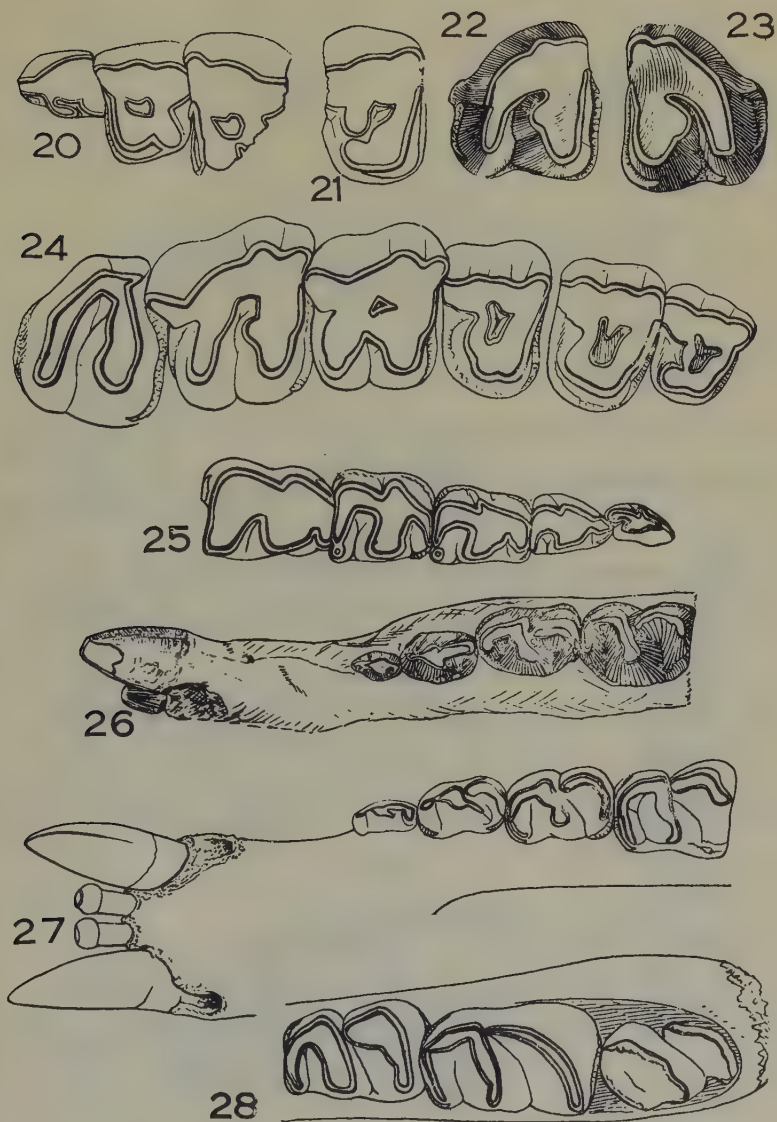
14. *Triplopus grangeri* ?, C. M. No. 3110,
R P 3/ - M 2/, x 1.
15. *Triplopus grangeri* ?, C. M. No. 3110,
L P /2 - M /3, x 1.
- Page 17
16. *Eotrigonias petersoni*, type, A. M. N. H. No. 2341,
L P 4/ - M 3/, x 1.
- Page 29
17. *Eotrigonias rhinocérinus*, type, Y. P. M. No. 13331,
L P 2/ - M 3/, x 1.
18. *Eotrigonias rhinocérinus*, type, Y. P. M. No. 13331,
R M 3/, x 1.
19. *Eotrigonias rhinocérinus*, type, Y. P. M. No. 13331,
R P /4 - M /3, x 1.
- Page 32



EXPLANATION OF
PLATE 5

FIGURE

20. *Trigonias osborni*, type, U. S. N. M. No. 3924,
L P 1-3/, x 1/2.
Pages 33-40
21. *Trigonias osborni*, type, U. S. N. M. No. 3924,
R P 3/, x 1/2.
22. *Trigonias osborni*, C. M. No. 95, R M 3/, x 1/2.
23. *Trigonias osborni*, C. M. No. 95, L M 3/, x 1/2.
24. *Trigonias osborni*, C. M. No. 98, R P 2/ - M 3/, x 1/2.
25. *Trigonias osborni*, U. S. N. M. No. 4815,
L P /1 - M /1, x 1/2.
26. *Trigonias osborni*, A. M. N. H. No. 9792,
R I /1 - P /4, x 1/2.
27. *Trigonias osborni*, C. M. No. 97,
lower incisors and R P /1-4, x 1/2.
28. *Trigonias osborni*, C. M. No. 97, R M /1-3, x 1/2.

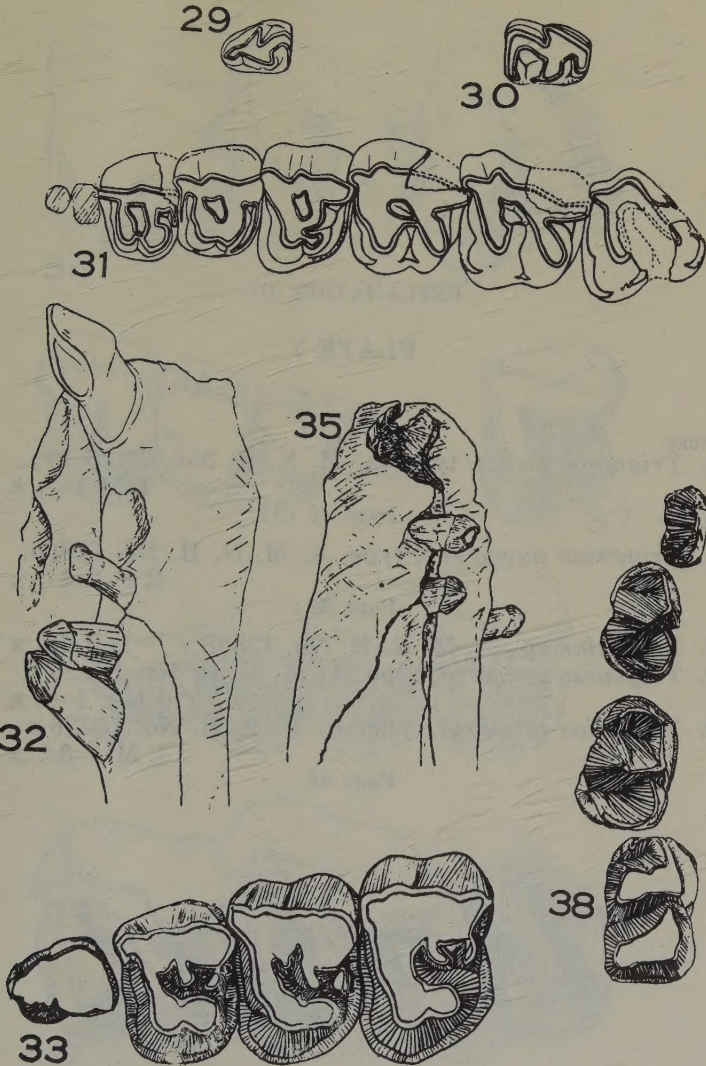


EXPLANATION OF

PLATE 6

FIGURE

29. *Subhyracodon gidleyi*, type, U. S. N. M. No. 11337,
R P /2, x $1\frac{1}{2}$.
30. *Subhyracodon gidleyi*, type, U. S. N. M. No. 11337,
L P /3, x $1\frac{1}{2}$.
31. *Subhyracodon gidleyi*, type, U. S. N. M. No. 11337,
L P 2/- M 3/, x $1\frac{1}{2}$.
Page 65
32. *Trigonias wellsi*, type, A. M. N. H. No. 13226 (1),
L I 1/, I 3/, d C 1/, C 1/, x $1\frac{1}{2}$.
33. *Trigonias wellsi*, type, A. M. N. H. No. 13226 (1),
L P 1-4/, x $1\frac{1}{2}$.
Page 46
35. *Trigonias paucidens*, type, A. M. N. H. No. 11865,
R-I 2-3/, L I 3/, x $1\frac{1}{2}$.
Page 51
38. *Trigonias gregoryi* ?, A. M. N. H. No. 13226 b,
R P /1-3, d P /4, x $1\frac{1}{2}$.
Page 49

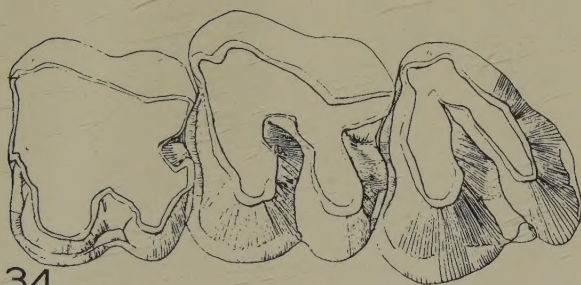


EXPLANATION OF

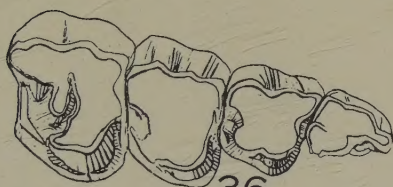
PLATE 7

FIGURE

34. *Trigonias wellsi*, type, A. M. N. H. No. 13226 (1),
LM 1-/, $\times 1\frac{1}{2}$.
Page 46
36. *Trigonias paucidens*, type, A. M. N. H. No. 11865,
RP 1-4/, $\times 1\frac{1}{2}$.
Page 51
37. *Trigonias* sp., A. M. N. H. No. 12308, LP 4/, $\times 1\frac{1}{2}$.
39. *Trigonias gregoryi*, type, A. M. N. H. No. 13226 a,
LP 1-4, $\times 1\frac{1}{2}$.
40. *Trigonias gregoryi*, type, A. M. N. H. No. 13226 a,
LM 1-3/, $\times 1\frac{1}{2}$.
Page 48



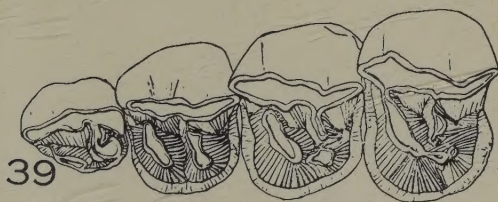
34



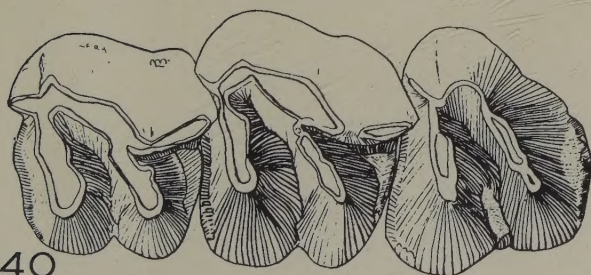
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37



39



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